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ARTICLE VII.

(Plates XVII and XVIII.)

THE OSTEOLOGY OF ELOTHERIUM.

BY W. B. SCOTT.

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Elotherium is one of the many genera of fossil mammals concerning which the growth of our knowledge has been exceedingly slow, and only of late has it become practicable to give a complete account of its bony structure. The genus was named in 1847 by Pomel ('47 *a*, *b*) and shortly afterward renamed *Entelodon* by Aymard ('48) from a better specimen, but for several years only the dentition was known and that imperfectly. In 1850, Leidy ('50, p. 90) described the first American species, but, not suspecting its generic identity with the European forms, he at first referred it to a new genus, *Archæotherium*. Leidy's material enabled him to give a fairly complete account of the skull. Kowalevsky, in 1876, described an imperfect skull found in France and he further showed that the feet were didactyl, a very unexpected fact in view of the pig-like character of the dentition. In this country Profs. Marsh and Cope have added materially to our knowledge of this remarkable animal (Marsh, '73, '93, '94; Cope, '79) and the former has published a restoration of one of the species. In spite, however, of this list of workers who have, from time to time, occupied themselves with the study of *Elotherium*, much still remains to be learned regarding its structure, and its phylogenetic relationships are even more obscure.

In the summer of 1894, Mr. H. F. Wells discovered in the White River Bad Lands of South Dakota certain bones, which, with the expenditure of infinite pains and skill, were excavated from the rock by Mr. J. B. Hatcher, and which proved to be a most remarkably complete skeleton of *Elotherium*. This beautiful specimen (Princeton Museum, No. 10885,) formed the subject of a preliminary communication which I made to the third International Zoölogical Congress, at Leyden (Scott, '96), and will be more fully described in the following pages. Except for a single thoracic vertebra (and perhaps a

few caudals) and part of the hyoid apparatus, the skeleton is complete; it is represented in Pl. XVII, which will enable the reader to judge of its unusual state of preservation. Additional material, belonging to several species, will also be made use of for purposes of of comparison, but the description will deal almost exclusively with the White River forms.

The Artiodactyla may almost be designated as the despair of the morphologist. So manifold are the forms which this puzzling group has assumed, and so variously are the characteristics of its minor groups combined, that the confusion seems hopeless. The only way in which this tangled skein can be unraveled and its many threads separated and made straight, is by the slow but sure method of tracing the phylogenetic development of each family step by step from its incipient stages. Many years must pass before sufficient palæontological material has been gathered to make this possible, but already some progress has been made in the work. Each successive form in a series, as soon as it is recovered, should be fully described and illustrated for the benefit of other workers, a necessity which must excuse the minuteness of detail into which the following description enters. For the sake of convenience the entire bony structure of the animal will be described, including those parts which are already well known, in order that the reader may be spared the trouble of searching through many scattered papers, written in several languages.

I. The Dentition.

The teeth of *Elotherium* are already familiarly known and require but a brief account here. The dental formula is I $\frac{3}{3}$, C $\frac{1}{1}$, P $\frac{4}{4}$, M $\frac{3}{3}$.

A. *Upper Jaw.*—The incisors, three in number, increase regularly in size from the first to the third, the latter being much the largest of the series; it has a conical or somewhat trihedral crown and resembles a canine in shape and appearance. In some individuals the crown of this tooth is worn in a peculiar manner, a deep groove or notch being formed on its posterior side, in a place where it cannot have been made by the attrition of any of the lower teeth. The other incisors have spatulate crowns, with blunted tips, the attrition of use wearing down the apices as well as the posterior faces of these teeth. This description applies more particularly to the larger White River species, such as *E. ingens* and *E. imperator;* in *E. mortoni* the upper incisors are of more nearly equal size and more conical shape. In all, the median incisors are separated from each other by a considerable notch, and the whole series is much more extended antero-posteriorly than transversely, the external incisor standing behind the second one. I $\frac{3}{3}$ is separated by a short diastema from the canine and at this point the premaxillary border is quite deeply notched to receive the lower canine.

The canine is a very large and powerful tusk, with a swollen, gibbous fang; the

crown is long, massive, recurved, and bluntly pointed; it is oval in section, and has a prominent posterior ridge.

The premolars are very simple in construction. The first three are well spaced apart and have compressed, but thick, conical crowns, without accessory cusps of any kind, and each is implanted by two fangs. In size, they increase posteriorly and $p\frac{3}{}$ has a decidedly higher crown than any other premolar. $P\frac{4}{}$ is smaller than $p\frac{3}{}$ in every dimension except the transverse, this diameter being increased by the addition of a large internal cusp (the deuterocone) and the crown is carried upon three fangs. In the smaller species of the genus, such as *E. mortoni*, $p\frac{3}{}$ and $p\frac{4}{}$ are placed close together, while in the larger forms these teeth are separated by a short space, and the diastemata between the other premolars and between $p\frac{1}{}$ and the canine are relatively somewhat greater, the enlargement of these teeth hardly keeping pace with the elongation of the muzzle. In the European species, *E. magnum*, the arrangement of the premolars is somewhat different, $p\frac{2}{}$, $\frac{3}{}$ and $\frac{4}{}$ forming a continuous series, while $p\frac{1}{}$ and $\frac{2}{}$ are quite widely separated.

The molars are relatively quite small; $m\frac{2}{}$ is the largest and $m\frac{3}{}$ the smallest of the series. The crowns are low and bunodont, bearing six tubercles arranged in two transverse rows. The hypocone, though functionally important, is decidedly smaller than the protocone, and structurally is still a part of the cingulum. Schlosser is, however, mistaken in supposing that there is any important difference between the American and the European species of *Elotherium* with regard to the position of the protocone. In $m\frac{3}{}$, which has a more oval crown than the other molars, the sexitubercular pattern is obscured by the development of numerous small tubercles upon the hinder half of the tooth. The cingulum of the molars is quite strongly marked, especially upon the anterior and posterior faces.

B. *Lower Jaw.*—The incisors resemble those of the upper jaw, except that they are of more nearly equal size and somewhat more spatulate shape; $i\frac{}{3}$ is little enlarged and is much smaller than the corresponding tooth in the upper jaw.

The canine is a very large, recurved tusk, like the upper one in size and shape; it bites between the upper canine and enlarged external incisor, the three teeth together making up a very formidable lacerating apparatus. An interesting hint as to the habits of this animal is given by a peculiar mode of wear of the lower canine which occurs in some well-preserved specimens. In these we find a deep groove on the posterior face of the tooth, beneath the enamel cap and close to the level of the gum. No other tooth can reach this point to cause such a mode of attrition, and the groove is doubtless due to the habit of digging up roots with the lower tusks; the pull of the roots, especially when covered with sand or other gritty material, would naturally wear such a groove.* The

* This ingenious and highly probable explanation of a somewhat puzzling fact was suggested to me by my colleague, Prof. C. F. Brackett.

same explanation applies to the curious notches sometimes worn in the external upper incisor. The numerous specimens examined do not indicate that there was any difference between the males and the females in the size of the canines, the tusks being invariably large and powerful. If, as here suggested, the canines served other purposes than those of weapons, the lack of any such sexual difference would be intelligible enough.

The premolars are very simple and quite like those of the upper series in shape; their crowns are massive, compressed cones, without additional cusps. The cingulum is usually prominent, but varies in the different species. $P\frac{}{3}$ is much the highest of the series, especially in *E. imperator*, where it rises to the full height of the canine, and gives a very characteristic appearance to the lower dentition. $P\frac{}{4}$ has its posterior face flattened, forming an incipient fossa with a number of small tubercles in it. $P\frac{}{3}$ and $\frac{}{4}$ stand quite close together, and $p\frac{}{1}$ is separated by a short space from the canine, while $p\frac{}{2}$ is isolated by considerable diastemata both in front of and behind it.

The lower molars are small in proportion to the size of the jaw and to the space occupied by the premolar series. In size they increase posteriorly, and they have a simple, quadritubercular pattern, the crowns surrounded by a strong cingulum. There is much variation in the development of the fifth or posterior unpaired cusp (hypoconulid); it is frequently absent and represented only by a strong cingulum, though sometimes it is present as a distinct cusp on $m\frac{}{1}$ or $m\frac{}{2}$. It is less commonly found on $m\frac{}{3}$ and only in the very large *E. leidyanum* is it well developed.

The Milk Dentition.—The temporary canines and incisors differ from the permanent ones only in size. It is uncertain whether the first premolar, in either jaw, has a predecessor in the deciduous series, none of the specimens distinctly showing such a predecessor. In one individual, however, the tip of $p\frac{1}{}$ is just visible in the centre of a large alveolus, from which a milk-tooth has apparently been shed. If this change does actually occur, it must take place at an early stage, and, on the whole, it seems probable that, at least in the upper jaw, the number of deciduous premolars is four. $Dp\frac{2}{}$ has a compressed, elongate, conical crown, without accessory cusps of any kind; it is carried on two widely separated fangs, and is isolated by diastemata both in front of and behind it. $Dp\frac{3}{}$ consists of three principal cusps. The antero-external cusp (protocone) is an acutely pointed pyramid, while the postero-external cusp (tritocone) is lower and smaller. The internal cusp (tetartocone) is posterior in position and placed on the same transverse line as the tritocone, while between the two is a small conule. The cingulum is distinct on the front and hind faces, obscure on the outer and absent from the inner face of the crown. $Dp\frac{4}{}$ is molariform, but differs somewhat from the molar pattern in the fact that the postero-internal cusp is even more distinctly an elevation of the cingulum and that the posterior conule is double.

The lower milk-premolars are even simpler than the upper; dp $\frac{}{2}$ and $\frac{}{3}$ are compressed and conical, without accessory cusps, but with serrate edges and sharply-pointed summit. Each of these teeth is supported upon two fangs. Dp $\frac{}{4}$ is of the usual artiodactyl type, consisting of three transverse pairs of cusps, of which the median pair is the largest, and the anterior pair the smallest. A small talon is formed by the elevation of the cingulum in the median line, behind the posterior pair of cusps.

This account of the milk dentition applies only to *E. mortoni;* I have not seen these teeth in the larger species.

Measurements.

	No. 11156	No. 10885	No. 11009	No. 11440
Upper dentition, length I 1 to M 3			?0.270	
" molar series, length	.118	.104	.064	.065
" premolar series, length	.238*	.175	.124	.113
" canine, ant.-post. diameter	.048*	.046	.032	
" " transverse diameter	.0385*	.042	.022	
" P 1, length	.030*	.024	.019	
" P 2, "	.038*	.038	.025	.023
" P 3, "	.041*		.028	.028
" P 4, "	.035*	.031	.0195	.018
" M 1, length	.035	.033		.020
" " width		.036		.019
" M 2, length	.042	.035	.025	.023
" " width		.039	.0235	.024
" M 3, length	.037	.034	.021	.021
" " width		.033	.022	.0215
Lower dentition, length I 1 to M 3	.432*			.261
" molar series, length	.121*	.108		.070
" premolar series, length	.211*	.192		.126
" P 1, length	.028*	.026		.017
" " height of crown	.026*			.019
" P 2, length	.031*	.033		.020
" " height	.038*			.023
" P 3, length	.046*	.043		.027
" " height	.061*			.031
" P 4, length	.046*	.037		.025
" " height	.044*			.020
" M 1, length	.037*	.031		.0215
" " width	.029*	.027		.013
" M 2, length	.0395*	.035		.0225
" " width	.036*	.030		.016
" M 3, length	.043*	.039		.0245
" " width	.037*	.028		.016

*No. 11161.

II. The Skull.

The skull of *Elotherium* is one of the most remarkable features of this very curious animal. It is characterized by great length and slenderness, with the supraoccipital and nasal bones lying in the same horizontal plane. The muzzle is exceedingly long and narrow, and tapers somewhat anteriorly, though expanded by the sockets of the great tusks; the orbit has been shifted far back, its anterior border being, in some species, over m $\frac{2}{}$, and in others above m $\frac{3}{}$. The cranium is short and of absurdly small capacity, which, with the great temporal openings, gives an almost reptilian appearance to the skull when viewed from above or below. The sagittal crest is very high and thin, and the zygomatic arches, though rather short, are enormously developed. One of the most peculiar features of the skull is the great, compressed plate which is given off from the ventral surface of the jugal and descends below the level of the lower jaw, and this grotesque appearance is further increased by two pairs of knob-like processes on the ventral borders of the mandible. The occiput (Pl. XVIII, Figs. 1, 2) is high and very broad at the base, but narrowing rapidly to the summit; above the foramen magnum it forms a broad, flat projection of almost uniform breadth, with a very deep fossa on each side of it.

The *basioccipital* is stout and rather short, keeled in the median ventral line and slightly contracted to receive the auditory bullæ; at its junction with the basisphenoid it forms a pair of small, roughened tubercles. The *exoccipitals* are very large bones, especially in the transverse direction along the base of the occiput, dorsally they narrow fast. Above the foramen magnum they form the very broad, prominent and nearly square projection which has already been mentioned; this is thick and is filled with cancellous bone, the fossa for the vermis of the cerebellum making but a slight depression upon its internal face. On each side of the projection is a large and deep triangular fossa, which, however, is not confined to the exoccipital, the periotic and squamosal both being concerned in its formation. The inferior part of the exoccipital extends widely outward, reaching to the line of the glenoid cavity, and ending in the large, prominent and massive, but not elongate paroccipital process. In this region the exoccipital is brought very close to the zygoma, but, ventrally at least, does not quite touch it, a narrow band of the tympanic intervening between them. The foramen magnum is strikingly small and of a transversely oval shape. The occipital condyles are relatively rather small, especially in the vertical dimension, laterally they are well extended, and they are widely separated both above and below. In the very large *E. imperator* the external angles of the condyles are abruptly truncated in a curious way, and bear flat articular surfaces, though in some individuals this truncation is found only on one side; while in the smaller species the condyles are of the usual form. The *supraoccipital* is a large bone, widest at the base (*i. e.*, the suture with the exoccipitals) and narrowing dorsally. Superiorly it is drawn out into two posterior wing-

like processes, such as are found in *Oreodon* and other White River ungulates. Between these wings the hinder face of the bone is concave and at the bottom of this concavity are two small, but profound pits. The supraoccipital is continued over upon the roof of the cranium and forms a part of the sagittal crest.

A considerable part of the *periotic* is exposed on the surface of the skull, at the bottom of the lateral occipital fossa, where it is enclosed between the exoccipital and the squamosal; it does not give rise to any distinct mastoid process.

The occiput of the European species, *E. magnum*, as figured by Kowalevsky ('76, Taf. XVII, Fig. 5), is different in many details from that which characterizes the American species. It has more of an hour-glass shape, not so wide at the base, more contracted in the middle and more expanded at the top, but with much less conspicuous wing-like processes, and it has no such projection above the foramen magnum, nor such deep lateral fossæ. The condyles are larger and of an entirely different shape, having their principal diameter vertical, instead of transverse. The paroccipital processes are longer, more compressed and not so widely extended laterally. The foramen magnum is large and of more nearly circular outline.

The *basisphenoid* is narrower than the basioccipital and is not keeled on the ventral surface, but is otherwise like that bone. So much of its course is concealed by the union of the palatines and pterygoids along the median line that its length cannot be determined, while the presphenoid is nowhere exposed to view.

The *tympanic* is very extensively developed (Pl. XVIII, Fig. 1). Part of it is inflated into an oval, somewhat flattened and rather small auditory bulla, which differs from that of *Hippopotamus* and of all existing suillines in being hollow and not filled up with spongy tissue. On the outer side of the bulla the tympanic is extended as a narrow strip, which broadens considerably between the squamosal and the exoccipital, with both of which it articulates suturally, as well as with the alisphenoid in front. The bulla itself terminates anteriorly in a blunt spine.

The *alisphenoid* is small and forms very little of the side of the cranium. It is most elongate antero-posteriorly along the ventral line, but has hardly any distinctly developed pterygoid process. At the line of the sphenoidal fissure, which notches but does not perforate the bone, the alisphenoid is narrowed, to expand again at its suture with the parietal and frontal. The *orbitosphenoid* is relatively rather large, but is low in the vertical dimension, and does not extend upward into the orbit proper. Two sharp ridges on the external face of the bone enclose a V-shaped groove, in which lie the optic foramen and foramen lacerum anterius.

The *parietals* are very large proportionately to the size of the cranium, but quite small as compared with the entire length of the skull; they roof in most of the cerebral

chamber, but toward the ventral side they rapidly contract, forming narrow strips between the squamosal and frontal. Throughout their length the parietals unite to form the very high, thin and plate-like sagittal crest, which is one of the most characteristic features of the skull. In the European species, *E. magnum*, this crest has a remarkably straight and horizontal course, but in the known American species it is gently arched from before backward. Large sinuses are developed in the parietals, so that the cerebral chamber is even smaller than it appears to be, when viewed from the outer side. These sinuses extend over the entire roof of the cerebral fossa, even invading the supraoccipital; they appear to be traversed by numerous small trabeculæ, the ends of which are seen, in the sagittal section, embedded in the matrix which fills the sinuses.

The *frontals* are much larger than the parietals. In the postorbital region they are very narrow, in conformity with the very small size of the brain, but at the orbits they expand widely to form the broad, lozenge-shaped forehead, which is convex from side to side, though slightly depressed, or "dished" in the middle; the supraciliary ridges are very inconspicuous. Anteriorly the frontals diverge to receive the nasals between them, sending forward long, pointed nasal processes, which, owing to the great elongation of the muzzle, are widely separated from the premaxillaries. The orbit is large and projects prominently outward; it is completely encircled by bone, the long and massive postorbital process of the frontal uniting suturally with the shorter process of the jugal. The orbits do not rise above the level of the forehead, as they do in *Hippopotamus*, and present more anteriorly, less directly outward, than in that animal. Mention has already been made of a groove on the orbitosphenoid, which terminates below and behind in the foramen lacerum anterius; this groove is continued upward and forward upon the frontal, steadily widening as it advances. The postero-superior ridge bounding the groove is the more prominent; it extends almost to the postorbital process, from which it is separated by a distinct notch, while the antero-inferior ridge dies away within the orbit. In most of the American species the forehead rises very gradually and gently behind to the sagittal crest, but in *E. ingens* the rise is much more sudden and steep. The frontal sinuses are large, giving the convex shape to the forehead which has been described; these sinuses appear to communicate with those formed in the parietals.

Except posteriorly, the *squamosal* forms but little of the side-wall of the cranium, its suture with the parietal curving abruptly downward and forward; its compressed and prominent hinder margin forms nearly the whole of the lambdoidal crest, though a continuation of it extends upward upon the supraoccipital, ending in the wing-like processes of that bone. The zygomatic process is enormously developed; it extends widely outward from the side of the skull as a massive, vertical plate, which is shaped much as in *Hippopotamus*, and is not continued forward as a broad, horizontal shelf, such as is found

in *Sus*. The superior border curves upward into a great, hook-shaped process, which resembles that seen in *Merycochœrus*, and gives a highly characteristic appearance to this region of the skull. That portion of the zygomatic process which is directed anteriorly is short and, though massive, is much less so than that which extends out laterally; in front it is received into a notch of the jugal. The glenoid cavity is large, transversely directed and quite deeply concave, though the postglenoid process is not strongly developed and is hardly more conspicuous than the preglenoid ridge. This disposition is unusual among the ungulates, but it occurs also in the Eocene genus *Achænodon* and in the modern *Dicotyles*. The glenoid cavities of the two sides are very widely separated, their *inner* margins lying external to the line of the paroccipital processes. The posttympanic process of the squamosal is small, and is closely applied to the paroccipital process. The shape of the zygomatic arches, together with the extreme narrowness of the cranium proper, causes the temporal openings to be very large and to appear widely open when the skull is viewed from above. These openings are, however, less extended transversely and more antero-posteriorly than in *Hippopotamus*, while in *Sus* they are hardly visible from above.

The *jugal* is a very remarkable bone and constitutes one of the most extraordinary features of the *Elotherium* skull. Posteriorly it is notched to receive the zygoma, and sends out a process along the ventral face of that bone, extending to the preglenoid ridge. The jugal forms the inferior half of the nearly circular orbit, and for this purpose its dorsal border is made deeply concave, giving off a stout postorbital process to meet that of the frontal, while anteriorly it is moderately expanded upon the face in front of the orbit, where it is wedged in between the lachrymal and the maxillary. The most peculiar feature of the jugal, however, is the immensely developed vertical plate, which descends from beneath the orbit downward and outward to below the level of the ventral border of the mandible, recalling the similar, but much less massive processes found in certain edentates, *e. g.*, *Megatherium*. These plates are laterally compressed, but quite thick, and when the skull is viewed from the front, they are seen to diverge quite strongly downward; their shape varies in the different species. In the very large forms from the Protoceras beds, such as *E. imperator*, the process retains its plate-like form throughout, its free end being only moderately thickened. This appears to be true also of *E. mortoni*, though my material is not sufficient to allow me to make this statement positively, but in the large species from the Titanotherium and Oreodon beds (*E. ingens*) it forms a club-like thickening at the tip, which in *E. ingens* is coarsely crenulate on the posterior border (see Pl. XVII). These processes are, so far as is yet known, quite unique among the hoofed mammals, and it is difficult to form even a conjecture as to what their functional significance may have been. Some misunderstanding has arisen as to the spe-

cies in which these jugal plates are found. Nothing is known concerning their presence or absence in the European representatives of the genus. Leidy's material gave him no reason to suspect their occurrence in the species described by him, and he consequently restored the zygomatic arches without them ('69, Pl. XVI). Marsh first discovered the processes in a skull of the species named by him *E. crassum*, and it has sometimes been assumed that they were more particularly characteristic of that form. As a matter of fact, they have been observed in all of the American species of which well-preserved skulls are known, viz., *E. mortoni*, *E. ingens*, and *E. imperator*, and, in all probability, all the American forms, at least, possessed them.

The *lachrymal* is a rather large bone and forms nearly half of the anterior boundary of the orbit. On the face it is expanded into quite a large plate, which articulates below with the jugal, in front with the maxillary, and above with the frontal, the long anterior process of which prevents any contact between the lachrymal and nasal. In *Hippopotamus* the very short, broad frontal has no anterior process, and so the nasal and lachrymal are connected, as they are also in *Sus*. Within the orbit the lachrymal is but little extended; the foramen is single, very small, and placed inside the orbital margin. The lachrymal spine is very low.

The *nasals* are narrow, slender and very much elongated. Their greatest width is at the anterior end of the nasal processes of the frontal, and here is also their greatest transverse convexity; from this point they narrow and flatten, both in front and behind. Anteriorly they contract very gradually and terminate in sharp points, with their free ends quite deeply notched. In *E. ingens* the nasals appear to be relatively shorter than in the other species. In *Hippopotamus* these bones have much the same shape as in *Elotherium*, but they narrow more abruptly behind the point of greatest width, and their free ends are not notched. In *Sus* the nasals are truncated posteriorly and in front their free tips project far beyond the borders of the premaxillaries.

The *premaxillaries* are very large and heavy bones, the horizontal or alveolar portion especially so. Posteriorly, this portion is constricted, forming a groove for the reception of the lower canine, expanding again in front to carry the large incisors. The palatine processes are not much developed, the very large incisive foramina leaving but little space for them; the spines are long and slender, extending behind the canine alveolus. The ascending ramus of the premaxillary is low and rises gradually behind, and though broad at first, it rapidly becomes very slender, terminating behind in a fine point. Though these bones in *Elotherium* have a very different appearance from the immensely enlarged premaxillaries of *Hippopotamus*, yet both may have been formed by divergent modifications of a common plan.

The *maxillary* is greatly extended antero-posteriorly, in correspondence with the

elongation of the whole muzzle; its facial portion is low, gradually diminishing in height forward, where its suture with the premaxillary forms a very gentle, sweeping curve. The longest suture of the maxillary is that with the nasal, the connection with the frontal being very short, owing to the extension of the lachrymal. Posteriorly, this bone projects but little beneath the orbit, which has an imperfectly developed floor, and the projection which it sends out to the jugal is much less massive than in *Hippopotamus*. The face gradually narrows forward, until it reaches the infraorbital foramen, expanding again in front of the foramen and swelling out into the prominent canine alveolus. The palatine processes of the maxillaries are long and narrow, and as the molar-premolar series of the two sides form almost straight and parallel lines, the bony palate is of nearly uniform width, slightly concave transversely, but almost plane antero-posteriorly. In front, these palatine processes are deeply emarginated by the large incisive foramina, and in the median line are still further notched to receive the long premaxillary spines.

The *palatines* make up but very little of the bony palate, forming only a narrow strip in front of the posterior nares, and narrow bands along the sides. The palatal notches are small and shallow. The *pterygoids* are elongate, but quite low; there are no hamular processes or pterygoid fossæ; the two bones meet suturally along the median dorsal line, completely concealing the presphenoid from view. The posterior nares are long, narrow and low, extending forward to the middle of $m\,\frac{2}{}$; the opening gradually contracts posteriorly, where it becomes very narrow, while the side-walls slope upward and die away upon the alisphenoids. Anteriorly the nares are divided by the very large *vomer*, which is distinctly visible, and which at its hinder termination expands into a transverse plate, articulating with the palatines. The meeting of the two pterygoids forms a small canal, which appears to overlie the whole length of the posterior nares and to open forward into the nasal chamber on each side of the vomer. This is a very exceptional arrangement, and I am unable to suggest what its functional meaning may be (see Pl. XVIII, Fig. 1, *c*).

The *cranial foramina* are, in some respects, quite peculiar. The condylar foramen is large and conspicuous, being placed well in front of the condyle; it is, however, smaller than in the specimen of *E. magnum* which Kowalevsky has figured. The close approximation of the paroccipital and stylomastoid processes, and the outward extension of the tympanic between them, have given a somewhat unusual position to the postglenoid and stylomastoid foramina; they are crowded close together at the postero-external angle of the auditory bulla, and both of them perforate the enlarged tympanic bone. The foramen lacerum posterius forms a long, narrow and curved slit at the postero-internal angle of the bulla, while the foramen lacerum medium and the opening of the eustachian canal occupy their ordinary position at the front end of the bulla. No distinct carotid canal is visible externally.

Kowalevsky inferred from the study of his specimen that the foramen ovale "nicht als selbständiges Foramen existirte, wie z. B. bei den Ruminanten, sondern mit dem For. lac. med. verschmolzen war, wie bei den heutigen Suiden und bei Hippopotamus" ('76, p. 433). This is probably a mistake; at all events, it is not true of the American species, in which the foramen ovale is a long, conspicuous opening, of oval shape, perforating the alisphenoid. As in the ungulates generally, there is no separate foramen rotundum, that opening being fused with the foramen lacerum anterius. The latter is a large and somewhat irregular opening, which notches the anterior border of the alisphenoid, passing between that bone and the orbitosphenoid. The optic foramen is small and well separated from the foramen lacerum anterius, lying in front of and at a slightly higher level than the sphenoidal fissure; it does not open so far forward as in *E. magnum*, and, in consequence, it does not form such a remarkably elongated canal as in the European species (see Kowalevsky, '76, Taf. XVI, Figs. 1 and 3, *dd*), but, on the other hand, it is far from being a simple perforation of the orbitosphenoid, such as occurs in the recent ungulates. This elongation of the optic canal should probably be correlated with the very small size of the brain, which would seem to have been relatively smaller than in the ancestors of the genus. Though the orbits are far behind their primitive position, the backward shifting of the optic tract would seem to have kept pace with the change in the position of the orbits.

The posterior palatine foramina are large and conspicuous openings, placed at the maxillo-palatine suture, and separating the two bones at these points; the palatine plates of the maxillaries are deeply grooved for some distance in front of the foramina. The incisive foramina are likewise large, invading both the maxillaries and the premaxillaries; indeed, their size prevents the development of any considerable palatine processes on the latter bones. These foramina are in very marked contrast to those of *Hippopotamus*, in which the enormously expanded and massive premaxillaries are perforated by two small and widely separated openings; in *Sus* also the incisive foramina are proportionately much smaller than in *Elotherium*. The infraorbital foramen is large and is separated from the orbit by a considerable interval, opening above the anterior border of $p\frac{3}{}$. In front of the foramen a deep groove channels the outer face of the maxillary for a short distance. The canal itself is much elongated, in correspondence with the great length of the jaws, and its posterior orifice, within the orbit, is very large. The lachrymal foramen, which is single, is quite small and is placed inside of the orbit.

The supraorbital foramen is subject to some variation in the different species. In *E. ingens*, from the Titanotherium beds, these openings are of good size, are placed quite near to the median line, and have well-marked vascular channels running forward from them. In specimens of *E. mortoni* from the Oreodon beds, and in the very large species

(*E. imperator*) from the Protoceras beds, the openings have become minute; they are shifted laterally and have no anterior grooves leading from them.

The *mandible* is not the least curious part of this remarkable skull. The horizontal ramus is extremely long and nearly straight, with an almost horizontal inferior border. The depth and thickness of the ramus vary considerably; even in skulls of the same length the mandible is decidedly more slender in some specimens than in others. The materials are, however, not yet sufficient to determine whether this difference is of a specific, sexual, or merely individual character. A remarkable knob-like process is given off from the ventral border of the mandible, beneath $p\frac{}{4}$, which is subject to much variation in shape and elongation, in accordance with the age and size of the animal. In young individuals still retaining the milk-dentition, the process is a mere rugose elevation, and in the adults of the smaller species it is hardly more than a knob, while in the large forms it becomes greatly elongated and club-shaped. No marked difference in this regard is observable between the species from the upper and those from the lower horizons of the White River formation, the process being relatively quite as long and prominent in *E. ingens* from the Titanotherium beds, as in *E. imperator* from the Protoceras beds, but in the huge John Day species it has become particularly long and heavy.

The symphysis is quite long and very thick and massive; the two rami are indistinguishably fused together and laterally expanded, so as to somewhat resemble the symphysis of *Hippopotamus*, though not attaining any such extreme degree of massiveness as in the modern genus. The chin is abruptly truncated and flattened, and rises very steeply from below; on each side, beneath or a little behind the canine alveolus, there arises from the ventral border a second club-shaped process, similar to, but much heavier and more prominent than the posterior process already described. These two pairs of knobs give to the jaw a highly peculiar and characteristic appearance; they form another of the enigmatical features of the *Elotherium* skull, for it is difficult to imagine what part they can have played in the economy of the animal.

The two inferior dental series pursue a nearly parallel course, diverging backward but little, but behind the molars the two rami turn outward and diverge rapidly, so that posteriorly they are very widely separated, in correspondence with the great interval between the glenoid cavities of the two squamosals. The angle of the mandible is prominent and descends below the ventral border of the horizontal ramus, much as in *Hippopotamus*, though not to the same extent. The ascending ramus is not high, but of considerable antero-posterior extent. The masseteric fossa is quite small, but very deeply impressed, and is situated quite high upon the side of the jaw. The condyle is relatively little raised above the level of the molar teeth, and it is sessile, hence inconspicuous, though it is large, transversely expanded, and strongly convex. The coronoid process

is strikingly low and small; it is of triangular shape, erect and not at all recurved, and is separated from the condyle by a very wide sigmoid notch. The mental foramen is small, single, and placed below $p\frac{2}{2}$.

Several of the *hyoid* elements are preserved in connection with the skeleton of *E. ingens* which forms the principal subject of this description. The stylohyal is quite long and slender; its proximal portion is laterally compressed and very thin, but moderately broadened in the fore and aft direction. For the distal two-thirds of its length the bone is thicker and of a compressed oval section, expanding into a club-shaped thickening at the lower end, which is excavated for the connecting cartilage. The ceratohyal is considerably shorter than the stylohyal, but of quite similar shape; its proximal end bears a cup-shaped expansion, beneath which it becomes very thin and much compressed, but broadened antero-posteriorly; the inferior part of the shaft is slender and oval in section, with another cup-shaped expansion at the distal end. The epihyal and basihyal have not been preserved. The thyrohyal is of remarkable length and slenderness, and obviously was not coössified with the basihyal; the bone is of subcylindrical shape, with expansions at the proximal and distal ends.

This hyoid apparatus does not resemble that of any artiodactyl with which I have been able to compare it. The elements of the anterior arch somewhat resemble those of *Hippopotamus*, but are more slender and elongate. In the modern genus, on the other hand, the thyrohyals are very short, and are ankylosed with the basihyal, a totally different arrangement from that which characterizes *Elotherium*.

From the foregoing description and accompanying figures it will be obvious that the skull of *Elotherium* is an extremely peculiar one. Among recent animals that of *Hippopotamus* approximates it most closely, and displays, with many striking differences, several decided and, it may be, significant resemblances. Some of these resemblances, such as the straight cranio-facial axis and the long sagittal crest, are of no particular importance, because they occur so very generally among the primitive ungulates of all groups. Other similarities, again, are not of this nature. The proportions of the cranial and facial regions, the degree of backward shifting of the orbits, the relations of the zygomatic and paroccipital processes, the broadening of the muzzle, and the general plan of skull construction, are all similar in the two genera. On the other hand, each genus has certain peculiarities correlated with its manner of life. Thus, the elevation of the orbits and the backward displacement of the posterior nares in *Hippopotamus* are adaptations to its aquatic habits. Doubtless the extraordinary peculiarities of *Elotherium*, such as the dependent processes of the jugals and the great knobs on the mandible, are of a similar nature, though, in the absence of the soft parts, it is difficult even to conjecture what their use may have been.

Measurements.

	No. 11156.	No. 10885.	No. 11009.	No. 11440.
Skull, extreme length on basal line	0.803	?0.618	?0.460	
" width across zygomatic arches (behind jugal process)	?.500	.443	.297	.264
" width at p ^{4}	.133	.140	.089	.082
Cranium, length to anterior border of orbit	.282	.288	.198	.193
Face, length to anterior border of orbit	.518	?.378	.270	
Occiput, breadth of base	.281	.252	.160	.158
" height	.158		.120	
Bony palate, length in median line		?.376	.247	
Zygomatic arch, length	.279	.271	.146	.146
Descending process of jugal, length	.330	.256		.126
Mandible, length	.659*	.608		
" height at coronoid process	.253*	.171		.107
" depth at p $_4$	.133*	.091		.052

* No. 11161.

III. The Brain.

Attention has been repeatedly called, in the foregoing description of the skull, to the extraordinarily small size of the brain-cavity. Even on viewing the skull externally, this smallness of the cranium proper strikes the observer immediately, and, in connection with the long, slender muzzle, gives the skull something of a reptilian aspect. When the cranium is sawn open in longitudinal section, it becomes apparent that the brain is even smaller than would be inferred from the external view alone, much of the space being, so to speak, wasted in the great frontal and parietal sinuses which overlie the whole cerebral chamber. In a large, full-grown skull this chamber will hardly contain an ordinary human fist.

The *olfactory lobes* are very large and are connected with the cerebrum by short thick olfactory tracts. The lobes are not at all overlapped by the hemispheres, but are entirely exposed for their whole length.

The *cerebral hemispheres* are relatively small, though they are, of course, much larger than the other segments of the brain; so short are they that they do not extend over the olfactory lobes in front, or the cerebellum behind. In shape, they are low and wide, narrowing gradually forward, but with blunt anterior termination. The frontal lobe is very small, for the frontals take but little share in the roof of the cerebral chamber. The parietal lobe, on the other hand, is relatively large and forms the greater part of the hemisphere, for there is, properly speaking, no occipital lobe, the occipital bones not taking any part in the formation of the cerebral fossa. The temporo-sphenoidal lobe is also quite large and prominent, but is short antero-posteriorly. The brain-cast shows that the

hemispheres were convoluted, but the convolutions are so feebly marked that they are hardly worth description. It is obvious, however, that the gyri were fewer and simpler than in any of the modern ungulates.

The *cerebellum* is rather small, though the cerebellar fossa has a vertical diameter not much less than that of the cerebral fossa. Antero-posteriorly the former is quite short and its transverse breadth is not great. This breadth is still further reduced by the relatively very large size of the periotic bones which extend freely into the fossa.

IV. The Vertebral Column.

The vertebral formula is: C 7, Th ? 13, L 6, S 2, Cd 15 +

The *atlas* (Pl. XVIII, Fig. 3) is very wide transversely, and at the same time it is of considerable antero-posterior extent, a shape which recalls that of *Anoplotherium*, rather than that of the recent ruminants or suillines. The anterior cavities for the occipital condyles are deep and wide, but low and depressed. Dorsally, these cotyles are widely separated by a broad, but not very deep emargination of the neural arch, nor do they approximate each other very closely on the ventral side, a notch of considerable width intervening between them at this point. The neural arch is thick and heavy, but short from before backward and quite narrow transversely; it is also low, not arching strongly toward the dorsal side, and nearly smooth, being free from any but the most obscurely marked ridges. The foramina perforating the arch for the first pair of spinal nerves are unusually large. The neural spine is rudimentary and forms only an inconspicuous tubercle. The neural canal is low and broad, forming a transversely directed ellipse. The inferior arch is considerably more elongated antero-posteriorly than the neural, and has but little transverse curvature, except laterally, where it rises to form the sides of the neural canal. The hypapophysis is represented by a small, backwardly directed tubercle, which arises from the hinder margin of the ventral arch, and occupies the same position as in the pigs, but is much less strongly developed. The articular surfaces for the axis are low and broad, and have a very oblique position, presenting inward toward the median line, almost as much as backward; they have also a slight dorsal presentation. In shape, they are very slightly concave and are surrounded by prominent borders. The facet for the odontoid is wide, and deeply concave in the transverse direction, but quite short antero-posteriorly. This facet is connected at the sides with those for the centrum of the axis, but distinct ridges are formed along the line of junction.

The transverse processes of the atlas extend out widely from the sides of the arch, attaining their greatest transverse breadth along the posterior line; they are also very long in the fore-and-aft direction, reaching far behind the surfaces for the axis. For most of their course the transverse processes have thin borders, but posteriorly the

margin becomes much thicker and more rugose. The vertebrarterial canal, which is notably small, occupies much the same position as in *Sus*, opening posteriorly upon the dorsal side of the hinder border. The anterior extension of the transverse processes has converted into foramina (atlanteo-diapophysial) the notches for the inferior branches of the first pair of spinal nerves. On the ventral face of each process is a large fossa, enclosed between the side of the inferior arch and the greatly thickened posterior border of the process. The resemblance in shape to the atlas of *Anoplotherium*, to which attention has already been called, affects more particularly the form of the transverse processes but they are more extended transversely than in that genus and are not so pointed at the postero-external angles.

The *axis* (Pl. XVIII, Fig. 4) is a short, but very massively constructed bone, which in general shape and appearance resembles that of *Hippopotamus*. The centrum is short, anteriorly very broad and depressed, but thickening posteriorly, and with a nearly circular and slightly concave hinder face. A strong and prominent keel runs along the ventral face of the centrum, enlarging backward, and terminating behind in a trifid hypapophysis. The odontoid process is short, heavy and conical, with no tendency whatever to assume the depressed and flattened shape which occurs in so many White River ungulates. The ventral articular surface of the odontoid seems like something superadded to the process itself, for it is clearly demarcated by a groove running all around it, and projects slightly in front of the body of the process. On the dorsal side of the centrum a broad and well-defined ridge runs backward from the odontoid along the floor of the neural canal. The atlanteal articular surfaces are very broad and low, not rising so as to enclose any part of the neural canal. They are very oblique with reference to the median line of the centrum, with which they form angles of about 45°. These surfaces are slightly convex in both directions, and ventrally they project much below the level of the centrum.

The transverse processes are short, thin and compressed, much less massive and widely extended than in *Hippopotamus;* they are perforated by very large foramina for the vertebral arteries. The pedicels of the neural arch are low and short, but very heavy; they are not pierced for the passage of the second pair of spinal nerves, as they are in *Hippopotamus* and in some of the pigs. The neural canal is decidedly small, especially its anterior opening; behind, it enlarges somewhat, particularly in the dorso-ventral dimension, the posterior opening being high and narrow, while in *Hippopotamus* it is low and broad. The neural spine is a large plate which is very thin in front, but becomes thick and massive behind, ending in a broad rugosity. This spine resembles that of *Hippopotamus*, but is not produced so far backward and does not overhang the third cervical. The postzygapophyses are large, slightly concave, and present obliquely

outward, as well as downward; their bases are separated by a broad and deep groove, which is continued upward upon the posterior side of the neural spine.

The *third cervical vertebra* also bears a considerable resemblance to that of *Hippopotamus*, differing only in some points of detail. The centrum is short, heavy and moderately opisthocœlous, depressed, but increasing posteriorly in vertical thickness. It bears a strong ventral keel, which terminates behind, as in the axis, in a trifid hypapophysis. The pedicels of the neural arch are not, as in the pigs, pierced by foramina for the spinal nerves; they are low and short, but very thick, and the neural canal is strikingly small. The dorsal side of the arch is short, broad and nearly flat. The neural spine is remarkably well-developed (when the anterior position of the vertebra is taken into account), rising as high as that of the axis. It is rather thin and compressed, although its base occupies the whole fore-and-aft length of the arch. From the base, however, it rapidly tapers upward and terminates in a small, rough tubercle. In *Hippopotamus* the third cervical has an even better developed neural spine, not higher, but broader and less tapering than in *Elotherium*. The prezygapophyses are large, oblique and somewhat convex; they are placed very low, so that their inferior margins are separated from the centrum only by narrow notches. The posterior zygapophyses are much larger and more prominent than the anterior pair; they are also less oblique in position and are raised higher above the centrum, corresponding to the posterior elevation of the neural arch. The transverse process is a compressed plate, which has no great vertical height, but is well extended from before backward, exceeding the centrum in length; the posterior portion of the process is thickened and recurved, ending in a rugose hook. The absence of any distinctly marked diapophysial element distinguishes this vertebra from the corresponding one of *Hippopotamus* and *Sus*, and in the latter genus the inferior lamella is more slender and rod-like, while the spinal nerves make their exit through foramina in the pedicels of the neural arch.

The *fourth cervical vertebra* is different, in many respects, from the third. The centrum is somewhat shorter and is less distinctly carinate on the ventral side, but is more decidedly opisthocœlous. The neural arch is remarkably short in the antero-posterior dimension, so that the articular faces of the postzygapophyses actually extend forward beneath those of the anterior pair, which gives to the pedicel of the neural arch, when seen from the side, a curiously notched appearance. The neural spine is higher, but more slender and recurved than that of the third cervical. The transverse process is altogether different in shape from that of the latter. It has, in the first place, a very prominent diapophysial element, which projects outward as a heavy, depressed bar, thickened, rugose, and slightly upcurved at the distal end. In the second place, the inferior lamella is much higher vertically, but decidedly shorter from before backward.

In *Hippopotamus* and in *Sus* this vertebra is very similar to that of *Elotherium*, but the neural spine is notably heavier.

The *fifth cervical vertebra* has an even shorter neural arch than the fourth and a much higher neural spine. The spine tapers rapidly from the base upward and becomes very slender, but it is nearly straight and only slightly recurved. The neural canal is somewhat larger than in the fourth vertebra, but, as in all the cervicals, it is strikingly small as compared with the size of the vertebra as a whole. The diapophysis is strong and prominent, but more slender than on the preceding vertebra, while the inferior lamella, though relatively short from before backward, has attained great vertical height and is strongly everted. In *Elotherium* the fifth vertebra is of the same type as the sixth, whereas in *Hippopotamus* it more nearly resembles the fourth.

The *sixth cervical* is very like the fifth, but displays certain obvious differences. Thus, the neural arch is even shorter antero-posteriorly, and the neural spine is higher, heavier and much more strongly recurved. The postzygapophyses are decidedly smaller and are very characteristic in their markedly oblique position, for they rise steeply backward in a way that occurs in none of the other vertebræ. The diapophysis is shorter but heavier than that of the fifth, while the inferior lamella is of similar shape, but larger, higher and with the free margin more thickened. In *Hippopotamus* this vertebra has much the same construction as in *Elotherium*, but the spine is shorter and more massive and the inferior lamella is much larger. In *Sus* the sixth cervical bears considerable resemblance to that of the White River genus.

The *seventh cervical* is characterized by the height and thickness of the spine, which in these respects much exceeds that of the sixth. This spine tapers superiorly, but expands again at the tip into a rough tubercle. The posterior zygapophyses stand at a higher level than the anterior pair and are unusually concave. The peculiarities seen in the postzygapophyses of the sixth and seventh vertebræ are to provide for the curvature of the neck, which changes its direction at this point. From the occiput to the sixth cervical the neck is nearly straight and inclines downward and backward, while the seventh vertebra begins the rise which culminates in the anterior thoracic region. This change in direction requires greater freedom of motion, which is supplied by the modification of the zygapophyses upon the vertebræ mentioned. The transverse process is, as usual, not perforated by the vertebrarterial canal; it is rather short, but heavy and much expanded at the distal end. On the posterior face of the centrum are large facets for the heads of the first pair of ribs. In *Hippopotamus* the neural spine of the seventh cervical is relatively much longer and heavier than in *Elotherium* or in *Sus*.

As a whole, the neck of *Elotherium* is short and massive, with very strongly developed processes for muscular and ligamentous attachments, as are indeed necessitated

by the immense weight and length of the head. Among recent artiodactyls *Hippopotamus* has cervical vertebræ most like those of *Elotherium*, though there are many differences in the details of construction. The most apparent of these differences lies in the greater and more uniform height and thickness of the neural spines in the modern genus. Doubtless the even more exaggerated massiveness of the skull in the latter is the occasion of this increased development of the cervical spines. In *Sus* the perforation of the neural arches for the passage of the spinal nerves constitutes an important difference from *Elotherium*.

The *thoracic vertebræ* would appear to have numbered thirteen, though this point cannot, as yet, be determined with entire certainty, and while the thoraco-lumbar vertebræ were, in all probability, nineteen in number, as is well-nigh universal among the artiodactyls, yet there were doubtless variations in the number of ribs, as is very frequently the case among existing animals.

The first thoracic has a rather small centrum, with decidedly convex anterior and nearly flat posterior face; the facets for the rib-heads are very large and deeply concave. The transverse process is rather short, but very large, heavy and rugose, and bears an unusually large, concave facet for the tubercle of the first rib. The prezygapophyses are of the cervical type, but present more obliquely inward than in the vertebræ of the neck, while the postzygapophyses are, as in the other thoracics, placed upon the ventral side of the neural arch. The neural canal is high and narrow and its anterior opening has assumed a cordate outline. The neural spine is inclined strongly backward, much more so than that of the seventh cervical, and though laterally compressed it is extremely high, broad and massive, greatly exceeding in all its dimensions that of the last neck vertebra.

The anterior six thoracic vertebræ (see Pl. XVIII, Fig. 5) are very much alike in appearance. The first three have broader and more depressed centra, which in the others become deeper vertically and more trihedral in section. The transverse processes are very large and prominent and carry large, deeply concave facets for the rib tubercles. The neural spines are very high, thick and heavy, and are strongly inclined backward, with club-shaped thickenings at the tips. At the seventh thoracic begins a rapid reduction in the length and weight of the spines, a process which reaches its culmination on the eleventh vertebra, which has a remarkably short, weak and slender spine. This arrangement results in a great hump at the shoulders, somewhat as in *Titanotherium*, though in a less exaggerated form. In both genera, the length of the anterior thoracic spines should be correlated with the great elongation and weight of the skull which requires immense muscular strength in the neck and shoulders. *Hippopotamus* has no such hump, but this is probably explained by its largely aquatic habits.

A change in the character of the facets for the rib tubercles occurs simultaneously with the shortening of the neural spines; they suddenly become much reduced in size and are plane instead of concave. The transverse processes, however, remain very large and prominent as far back as the eleventh thoracic. In no case are these processes perforated by vertical canals, such as occur in *Sus*. The twelfth thoracic is the anticlinal vertebra and has a nearly erect spine of lumbar type, though somewhat more slender than in the true lumbars. On the thirteenth the spine is quite like that of the lumbars and inclines slightly forward. Transverse processes are absent from the last two thoracic vertebræ, which display the feature, very unusual in an ungulate, of large and conspicuous anapophyses.

As far back as the eleventh vertebra the zygapophyses are of the ordinary thoracic type; they are small, oval facets, the anterior pair on the front of the neural arch and presenting upward, the posterior pair on the hinder part of the arch and presenting downward. On the eleventh thoracic a change takes place; the anterior zygapophyses are as before, but the posterior processes are flat and present obliquely outward, rather than downward, the two together forming a prominent, wedge-shaped mass. The prezygapophyses of the twelfth vertebra are correspondingly modified; they present obliquely inward and together constitute a cavity which receives the wedge-like projection from the eleventh. Prominent metapophyses also make their appearance on the twelfth thoracic. The posterior zygapophyses of the latter and both pairs of the thirteenth are of the cylindrical, interlocking type characteristic of the lumbars. These processes are remarkably complex and in a fashion that does not occur in *Hippopotamus*, but is found in *Sus* and many of the Pecora. The complexity is occasioned by the development of large episphenial processes, which give an additional articular surface above the zygapophyses proper; in section these processes have an S-like outline, and they constitute a joint of great strength.

The *lumbar vertebræ* (Pl. XVIII, Fig. 6), almost certainly six in number, have rather short, but massive centra. In the anterior part of the region the centra are somewhat cylindrical in shape, but they become more and more depressed and flattened as we approach the sacrum. The neural canal is broad and very low, especially in the posterior part of the region. The neural spines are inclined forward and are of moderate height; they are broad antero-posteriorly, but thin and laterally compressed, except at the tips, where they are thickened. The spine of the last lumbar is a little different from the others in being more erect and slender. Episphenial processes are present on the first, second and sixth vertebræ, but not on the third, fourth or fifth. These processes are apt to be somewhat asymmetrical and better developed on one side than on the other, and it is probable that more extensive material would show them to be subject

to much individual variation. Metapophyses are prominent only on the first and second lumbars, rudimentary on the third and absent from the others. The transverse processes are very feebly developed in proportion to the size of the vertebræ. On the first lumbar they are short and straight, and gradually increase in length up to the fifth, but in all they are strikingly thin and slender. The last lumbar has transverse processes of unusual length, space for them being obtained by the sudden eversion of the anterior ends of the ilia, but even here they are weak.

The trunk-vertebræ of *Hippopotamus* are much more massively constructed than those of *Elotherium*, the decrease in length of the thoracic spines posteriorly is more gradual, while the neural spines and transverse processes of the lumbars are much longer and in every way heavier. The thoraco-lumbar series of *Sus* bears considerable resemblance to that of *Elotherium*, but in the former the transverse processes of the thoracic vertebræ are perforated by vertical canals, and those of the lumbars are much longer and stouter.

The *sacrum* consists of two vertebræ only. The first has a broad, depressed centrum and very large pleurapophyses, which carry most of the weight of the ilia, though the second sacral has also a limited contact with the pelvis. On the first vertebra the prezygapophyses are very well-developed and have large episphenial processes to receive those of the last lumbar. The two neural spines are coössified into a high but short ridge. The second sacral has a very much smaller and especially a narrower centrum than the first, and retains moderately complete postzygapophyses.

In *Hippopotamus* and in *Sus* the sacrum is relatively much larger than in *Elotherium*, and consists of at least four vertebræ, sometimes even as many as six. Even in aged individuals of the White River genus I have not seen more than two vertebræ in the sacrum.

The *caudal vertebræ* (Pl. XVIII, Figs. 7, 8, 9), of which fifteen are preserved in association with one individual, indicate a tail of only moderate length, and present a number of peculiarities. The first caudal has somewhat the appearance of a miniature lumbar; its centrum is short, broad and depressed, with quite strongly convex faces; the neural canal is relatively large and a distinct, though small, neural spine is present. The zygapophyses, especially the anterior pair, are large and prominent and project much in front of and behind the centrum. The transverse processes are quite long and heavy, and are directed outward and backward. A pair of tubercles on the ventral side of the centrum represent rudimentary hæmapophyses.

The succeeding caudal vertebræ resemble the first in a general way, but passing backward, the centra become more and more slender and elongate, while the neural canal diminishes in size, and the various processes are reduced. The hæmapophyses, on the

other hand, increase in size and on the (?) fifth vertebra they curve toward each other, almost meeting and enclosing a canal, which continues as far back as the (?) eighth vertebra, behind which the hæmapophyses are again reduced. The middle portion of the tail is composed of very long, cylindrical vertebræ, which in shape strikingly resemble those of the great cats, and which are proportionately much longer, though apparently less numerous than those of *Anoplotherium*. At the anterior end of each vertebra are six prominent, nodular processes, the zygapophyses, transverse processes and hæmapophyses respectively. Posteriorly the centra become more and more slender, but are not much diminished in length, for what appears to be the penultimate vertebra is nearly as long as those in the middle region. The various processes are, however, reduced to very insignificant proportions. The last vertebra has its anterior portion shaped like that of its predecessor, but it rapidly tapers behind to a smooth, slender, compressed and subcylindrical rod, with a club-shaped thickening at the end. As I have seen but a single specimen of this curious vertebra, I cannot feel quite confident that its shape is a normal one and not due to some injury or morbid process.

The tail of *Hippopotamus* is of about the same relative length as that of *Elotherium*, but the individual vertebræ are very different, being all shorter and heavier, and diminishing in size more gradually to the end. In *Sus* the caudal vertebræ are somewhat more like those of *Elotherium*, but none of them have such slender elongate centra. Little is known concerning the caudals of *Anthracotherium*. Kowalevsky says of them: "Von den Schwanzwirbeln liegt mir nur ein einziges vor. Obwohl seine Erhaltung sehr mangelhaft erscheint, kann man doch aus diesem kleinen Stück den Schluss ziehen, dass der Schwanz bei den Anthracotherien kurz war und somit gar keine Aehnlichkeit mit dem sonderbar langen Schwanze der Anoplotherien hatte" ('73, p. 333; Taf. x, Fig. 36). The vertebra described by Kowalevsky is an anterior caudal and is much smaller and in every way more reduced than the corresponding ones of *Elotherium*. Among existing artiodactyls, it is the giraffe which most resembles the White River genus in the peculiar character of its caudal vertebræ.

Measurements.

Atlas, length	0.160
Atlas, greatest width	.270
Axis, length of centrum	.085
Axis, length of odontoid	.026
Axis, anterior breadth	.109
Axis, posterior breadth	.054
Third cervical, length	.066
Seventh cervical, length	.056
First thoracic, length	.051

Measurements.

Fifth thoracic, height of neural spine	.291
First lumbar, length	.050
Sixth lumbar, length	.048
Sixth lumbar, breadth across transverse processes	.176
Sacrum, length	.098
First sacral, width of centrum	.068
Second sacral, width of centrum	.025
Anterior caudal, length	.032
Median caudal, length	.063

V. The Ribs and Sternum.

The *ribs* of *Elotherium* are decidedly smaller and lighter and indicate a less capacious thorax than we should expect to find in such a large animal, a fact which adds to the apparent height of the skeleton, because of the long interval between the thorax and the ground.

The first rib is short, subcylindrical proximally, but broadening considerably at the distal end; it has only a slight lateral curvature, appearing nearly straight when viewed from the front, but it arches moderately backward. The head is large and compressed, and is separated by a deep and narrow notch from the very large and conspicuous tubercle, which is also compressed laterally. The ribs increase gradually in length up to the seventh or eighth of the series, and the posterior five, though successively shortening, retain a considerable relative length throughout. The first five or six ribs are laterally compressed and of moderate breadth, but the posterior part of the thorax is composed of very slender and subcylindrical ribs, very different from those which we find in most ungulates, except in the more primitive groups. The tubercle reaches its maximum of size and prominence on the third rib, behind which it gradually diminishes in size and becomes more and more widely separated from the head, and more sessile in position. On the twelfth and thirteenth pairs the tubercles are absent, corresponding to the lack of transverse processes on the twelfth and thirteenth thoracic vertebræ.

In *Hippopotamus* the ribs are relatively very much longer, broader and heavier than those of *Elotherium*, and grow broader toward the hinder end of the thorax, where the great bony slabs are in the sharpest possible contrast to the slender and subcylindrical rods of the extinct genus. In *Sus* the ribs are more like those of *Elotherium*, but they have not such a regular and symmetrical curvature as in the latter.

The *sternum* of *Elotherium* is a very remarkable structure, and although it is of distinctly suilline type, it is, nevertheless, not altogether like the sternum of any known genus, recent or fossil. The presternum, or manubrium, forms a very large, thin, compressed and keel-shaped plate, which is especially remarkable for its great vertical depth,

this dimension exceeding the antero-posterior length, and is proportionately much greater than in *Hippopotamus* or the modern suillines. The body of this segment is extremely thin, but the anterior border, and to some extent the ventral border also, is thickened and rugose. The facets for the first pair of sternal ribs form prominences, which are situated near together and close to the postero-superior angles of the segment, so that nearly the entire length of the latter projects in front of the first pair of ribs.

Of the mesosternum four segments and a part of the fifth are preserved. The first segment somewhat resembles the presternum in shape, being short, narrow and very deep; the dorsal border is much thicker and wider than any other part of the segment, and the ventral border is also thickened, though in a less marked degree. Posteriorly, this element becomes somewhat wider and shallower. The second segment of the mesosternum is decidedly broader and shallower than the first, but still retains a very unusual degree of vertical depth. Both the dorsal and ventral surfaces are much broadened, while the body of the bone is a thin, vertical plate, which connects the horizontally directed dorsal and ventral borders, giving a cross-section somewhat like that of an I-beam. In the third segment these progressive changes are carried still farther, and the bone becomes very distinctly broader and lower than the second segment. The dorsal and ventral borders still project much beyond the vertical connecting plate; this plate, however, is much thicker transversely than in the preceding segment. The ventral surface is rendered quite strongly concave by the elevation of its lateral borders. In part, this concavity may be due to the pressure which has somewhat distorted the entire sternum, but the ventral groove is so symmetrical that it can hardly be altogether due to distortion. The fourth and fifth segments exhibit similar changes, each one being broader and lower than the one in front of it; the vertical plate becomes very much thicker and the ventral groove more widely open. Though the specimen is of an animal past maturity, yet the last three segments distinctly show the median suture, along which their lateral halves united.

In *Hippopotamus* the breast-bone is quite like that of *Elotherium*, but the presternum is longer and not of such exaggerated depth, and the rib-facets are placed much nearer to the anterior end, while the mesosternum consists of fewer, broader and shallower segments. In *Sus* the sternum is still more like that of *Elotherium*, but has a decidedly longer and lower presternum.

VI. The Fore Limb.

The fore limb of *Elotherium* is quite elongate and, in connection with the shallow thorax, and very long neural spines of the anterior thoracic vertebræ, it gives to the skeleton a somewhat stilted appearance.

The *scapula* is remarkably high, narrow and slender, at least in the White River species, while in the John Day forms there is reason to believe that its proportions are quite different. The glenoid cavity forms a narrow, elongate oval, with its long axis directed antero-posteriorly, and is not very deeply concave. The coracoid is a large, but not very conspicuous rugosity, which sends off from its inner side a compressed, hook-like process; when the shoulder-blade is seen from the external side, this process is concealed from view. The neck of the scapula is broad and rather thick, and there is no distinct coraco-scapular notch. The coracoid border in its upward course inclines forward but little, and for the upper one-third of its height curves gently backward, to join the suprascapular border, which is exceedingly short. The glenoid border is more oblique, and inclines backward and upward at a moderate angle. The spine is shifted far forward, dividing the blade very unequally, so that the prescapular fossa is very much smaller than the postscapular. Indeed, the distal one-third of the shoulder-blade can hardly be said to have any prescapular fossa at all. The spine itself is rather low, and for much of its course its free border is curved backward and thickened to form a massive metacromion. The acromion is very short and inconspicuous, ending considerably above the level of the glenoid cavity.

The scapula associated with the large species of *Elotherium* from the John Day beds, which Cope has described under the name of *Boöchœrus* ('79, p. 59), is very different in shape from that of *E. ingens* from the White River, to which the description in the preceding paragraph more particularly applies. The blade is very much broader, both fossæ widening rapidly toward the dorsal end; these fossæ are of nearly equal width and the spine is placed almost in the middle of the blade. There can be little doubt that this scapula is properly referred to the incomplete skeleton with which it was found associated. Aside from its similarity in color and texture to the rest of the skeleton, there is no other animal known from the John Day horizon to which so large a scapula could belong.

The shoulder-blade of *Hippopotamus* is much broader, in proportion to its height, than that of *E. ingens;* the coracoid is more prominent and the coraco-scapular notch is distinctly marked; the postscapular fossa is somewhat larger than the prescapular, but the difference is much less extreme than in the White River species, the spine occupying a more median position; the acromion is much the same in the two forms, but the metacromion is larger in the fossil. In *Sus* also the scapula is relatively broader than in *E. ingens*, and, in particular, it has a wider prescapular fossa, but is without any distinct coraco-scapular notch. The spine rises from the suprascapular border very steeply to the high (but much smaller) metacromion, and then descends gradually to the neck, without forming an acromion. In spite of these differences, the resemblance in the character of the scapula between *Sus* and *Elotherium* is unmistakable.

The *humerus* is relatively long, but is, at the same time, a massively constructed bone. The head is large and very strongly convex, especially from above downward, although it is not set upon a very distinct neck, nor does it project far behind the plane of the shaft. The external tuberosity is very large, forming a massive and roughened ridge, which runs across the whole anterior face of the head and rises toward the internal side, where it terminates in a high, thick and recurved hook, overhanging the bicipital groove. The internal tuberosity is very much smaller, but is, nevertheless, quite prominent; it likewise projects over the bicipital groove, which is very broad and deeply incised into the bone. The great transverse breadth of the external tuberosity displaces the groove far toward the internal side of the humerus. The shaft is long and heavy; its proximal portion has a great antero-posterior diameter, and its transverse thickness, though less, is still very considerable. The fore-and-aft diameter gradually diminishes downward, until the shaft assumes an almost cylindrical shape, below which point it begins to expand transversely. The deltoid ridge is rugose and prominent, and runs far down upon the shaft, but forms no deltoid hook. The distal end of the shaft is very heavy, being both broad and thick. The supratrochlear fossa is low, wide and shallow, while the anconeal fossa is very high, narrow and deep, its depth being much increased by the great production of the posterior angles of the distal end. The supinator ridge is rough, heavy and prominent. The trochlea, which is very completely modernized, in correspondence with the advanced differentiation of the ulna and radius, is somewhat obliquely placed with reference to the long axis of the shaft, descending toward the ulnar side. The trochlea differs very markedly from that of such primitive artiodactyls as *Oreodon* and *Anoplotherium;* it is high, full and rounded and is divided into two unequal radial facets, of which the inner one is decidedly the larger. The intercondylar ridge, which, in most primitive artiodactyls, forms a broad and rounded protuberance, is, in *Elotherium*, compressed into a sharp and prominent ridge, and shifted well toward the external side. The internal epicondyle, which is so largely developed in *Oreodon* and other early artiodactyls, has practically disappeared.

The humerus of *Hippopotamus* is relatively much shorter and more massive than that of *Elotherium;* the external tuberosity is not extended so far across the anterior face of the bone and the bicipital groove is, in consequence, not shifted so far toward the inner side; the deltoid ridge is much better developed and gives rise to a prominent deltoid hook. In the existing species of *Hippopotamus* the intercondylar ridge is narrower and less conspicuous, but in a Pliocene species from the Val d'Arno it has quite the same appearance as in *Elotherium* (see de Blainville, Ostéographie, Hippopotamus, Pl. V). The epicondyles are much more prominent than in the latter, and the postero-internal border of the anconeal fossa projects much more than does the

external border, while in *Elotherium* this difference is decidedly less marked. In *Sus* the humerus resembles that of the White River genus in form, but is proportionately very much shorter; the deltoid ridge is shorter and less prominent, while the supinator ridge and the epicondyles are more so.

The *radius* and *ulna* (Pl. XVIII, Fig. 10) are firmly coössified in all the known species of *Elotherium*, though the suture between them is clearly marked, even in old animals. The radius is relatively very long, but rather slender; the head is quite thick, but of only moderate breadth, projecting most toward the external side. The humeral surface is composed of three connected facets, of which the internal one is much the largest and bears an elevated ridge for the corresponding depression on the humeral trochlea. The groove for the intercondylar ridge of the latter is quite broad and notches the anterior border of the radius. The shaft is rather narrow transversely, but quite thick and heavy, and arches forward but moderately; the distal portion is broadened and thickened and bears upon its dorsal face a deep tendinal sulcus, bounded by very prominent ridges. The distal face is quite broad, but without much dorso-palmar extension, and carries two well-distinguished carpal facets, which pursue an oblique course, from before backward and inward. The scaphoidal facet, which is the smaller of the two, is concave in front, saddle-shaped behind, and is reflected up upon the posterior face of the bone. The facet for the lunar is much larger than that for the scaphoid, and has a somewhat similar shape, but the anterior concavity is not so deep, and the articular surface is carried much farther up upon the palmar side of the radius. The radius has no contact with the pyramidal.

In *Hippopotamus* the forearm bones are ankylosed, though somewhat less intimately than in *Elotherium*. The radius is very short, broad and thick, and is almost straight. The external facet for the humerus is larger and more concave and the carpal facets are of more nearly equal size, while that for the lunar rises much more steeply toward the ulnar side. In *Sus* the two bones are separate, and the radius is short, very heavy and arched forward; its distal end is much more thickened than in *Elotherium*, the facet for the scaphoid is relatively larger, while that for the lunar is smaller and is extensively reflected upon the palmar face of the radius. In *Dicotyles* the ulna and radius have coalesced even more completely than in *Elotherium*.

The *ulna* has a very long, thick and prominent olecranon, which projects far behind the plane of the shaft. The process is convex on the outer side and concave on the inner, thickened and club-shaped at the free end, which displays a broad, shallow sulcus for the extensor tendons. The sigmoid notch is deep and the coronoid process prominent, as is required by the great depth of the anconeal fossa on the humerus. The articulation of the ulna with the latter is confined to the posterior and superior aspects of the humeral

trochlea, no part of the articular surface on the ulna presenting proximally, for the radius occupies the entire distal aspect of the humerus. Only the proximal portion of the facet for the humerus extends across the entire breadth of the ulna; for the rest of its course this facet is confined to the inner side. The shaft of the ulna is somewhat reduced, but is not interrupted at any point and, indeed, it is quite stout for its entire length; its principal diameter is the transverse, the antero-posterior thickness being decidedly diminished. Below the head it narrows and then expands to its maximum breadth, from which point it narrows gradually to the distal end. On its external side the shaft is quite deeply channeled. The distal end is small and bears a saddle-shaped facet for the pyramidal, which is concave transversely and convex in the dorso-palmar direction; its external border is compressed and extends as a sharp edge behind the body of the bone, forming a concavity on the palmar face. The pisiform facet is continuous with that for the pyramidal. The ulna extends distally below the level of the radius and thus arises the very exceptional condition of an articulation between the ulna and the lunar. The facet for this carpal element is small and is entirely confined to the radial side of the ulna, the distal end of the latter not extending at all upon the proximal face of the lunar. In most artiodactyls in which the functional digits have been reduced to two, the radius tends to encroach more or less extensively upon the proximal face of the pyramidal, for which extension the diminution of the ulna makes a way. In *Elotherium* the arrangement is different, the ulna occupying the entire proximal surface of the pyramidal, and by extending below the level of the radius securing a lateral contact with the lunar. Indeed, this arrangement quite precludes the attainment of the more usual radial-pyramidal articulation.

The ulna of *Hippopotamus* is proportionately much shorter and in every way more massive than that of *Elotherium;* it also has a very much larger and more prominent olecranon, as would naturally follow from the immensely greater weight of body which requires support upon the limbs. There appears to be a slight disto-lateral contact between the ulna and the lunar; at all events, the radius does not extend over upon the pyramidal. In *Sus* the ulna is free throughout and its shaft is relatively much shorter and heavier than in *Elotherium;* the ulna and lunar do not come into contact. The ulna of *Dicotyles* is more reduced than that of the White River genus and the connections of the carpals with one another and with the metacarpus are upon quite a different plan.

Measurements.

Scapula, height	0.430
Scapula, greatest width	.245
Scapula, breadth of neck	.065
Scapula, glenoid cavity, ant.-post. diameter	.068

Measurements.

Scapula, glenoid cavity, transverse diameter	.050
Humerus, length	.405
Humerus, width of proximal end	.132
Humerus, thickness of proximal end	.128*
Humerus, width of distal end	.095
Radius, length	.350
Radius, width of proximal end	.074
Radius, width of distal end	.062
Ulna, length	.443
Ulna, length of olecranon fr. coronoid process	.103
Ulna, width of distal end	.037

VII. The Manus (Pl. XVIII, Fig. 11).

The principal facts of the structure of the fore foot have already been determined by Kowalevsky, but the material now at command permits a more complete account to be given. Certain differences also which obtain between the European and American representatives of the genus should not be passed over without mention.

The *carpus* of *Elotherium* is a curious one in many ways, and while modified to suit the didactyl condition of the foot, by the reduction of the lateral and enlargement of the median elements, it has yet retained many of its primitive characteristics.

The *scaphoid* is high and thick in the dorso-palmar direction, but very narrow transversely. The dorsal and internal (*i. e.*, radial) surfaces of the bone are very rugose, and on the palmar border, which is the narrowest part of the scaphoid, is a blunt and massive mammillary process. The articular surface for the radius is of unusual shape. It is divided into two parts, an antero-external and a postero-internal; the latter is much the larger and is saddle-shaped, convex transversely and concave in the dorso-palmar direction, while the former is convex and descends steeply toward the ulnar side. These two parts of the articular surface are continuous, but they meet at nearly a right angle, and their junction forms a ridge, which is the highest point of the scaphoid. On the ulnar side are three facets for the lunar; the largest one is proximal and dorsal, and is continuous with the surface for the radius, which it meets at almost a right angle; this facet is very oblique and presents distally as well as laterally, the scaphoid here forming a projection which extends over the lunar. The second lunar facet is dorsal and distal in position; it is small, nearly plane, and not very distinctly separated from the facet for the magnum. The third lunar facet is distal and palmar, and is placed upon the ulnar side of the mammillary process already mentioned; it is of oval shape and nearly flat. The contact between the scaphoid and the lunar is confined to these three points, and as the

*Somewhat reduced by crushing.

facets on both bones are more or less prominent, they are elsewhere separated by considerable interspaces. The distal side of the scaphoid is much narrower than the proximal and is occupied by facets for the trapezoid and magnum, no articular surface for the trapezium being apparent. The trapezoidal facet is considerably the smaller of the two, and is simply concave. The magnum facet is in two parts, a very slightly concave distal portion, and a somewhat smaller lateral portion on the ulnar face of the scaphoid.

In the European species figured by Kowalevsky ('76, Taf. XXVI) the scaphoid is somewhat broader than in the American forms. In both groups a remarkable resemblance to the scaphoid of *Anthracotherium* is observable, which extends to even the details of structure (see Kowalevsky, '73, Taf. XI, Fig. 38). As *Anthracotherium* is, however, a tetradactyl form, the scaphoid is somewhat broader in proportion to its height than that of *Elotherium*, though hardly so much so as would be expected. In *Hippopotamus* and *Sus* the scaphoid is of quite a different shape from that of the fossils, being distinctly shorter and wider.

The *lunar* is a very large and complex carpal, which exceeds the scaphoid in all of its dimensions, and especially in breadth. The radial facet is in two parts, continuing those which occur on the scaphoid; the anterior or dorsal part extends across the width of the bone and is very convex antero-posteriorly, while the palmar portion is very much larger and is concave in the same direction. The dorsal border rises steeply toward the ulnar side, where the lunar is drawn out into a blunt, projecting, hook-like process, which extends over the pyramidal, as the scaphoid does over the lunar. On the radial side are three facets for the scaphoid, corresponding to those on the latter, which have already been described. The palmar face is greatly extended transversely, and, though lower, is much broader than the dorsal surface. On the ulnar side are two facets for the pyramidal, which constitute an interlocking joint of unusual firmness and strength. One of these facets is proximal and dorsal and overlaps the pyramidal; the second, which is very much larger, is palmar and distal in position, and has a saddle-like shape; it interlocks closely with a similar facet upon the pyramidal. When seen from the front, the contact between the lunar and the magnum appears to be entirely lateral, but as it passes toward the palmar side, the magnum facet broadens, becomes very concave, and assumes a distal position. The unciform facet is also oblique and the beak between the two is not in the median, but shifted far toward the radial side. Dorsally the unciform facet is considerably wider than that for the magnum, but on the palmar side these proportions are reversed.

The lunar of *E. magnum* figured by Kowalevsky resembles that of *E. ingens*, except that its proximal surface does not rise so steeply toward the ulnar side and does not

project over the pyramidal. The lunar of *Anthracotherium* (see Kowalevsky, '73, Taf. XI, Fig. 37) is like that of *Elotherium*, but is narrower, especially its palmar face, and much thicker, and the distal beak is more nearly in the median line. In *Hippopotamus* the lunar is broad and rests almost equally upon the magnum and the unciform, as it does also in *Sus*.

The *pyramidal* quite resembles the scaphoid in shape, but is much broader, not so thick antero-posteriorly, and generally of a more rugose and massive appearance. In view of the reduced lateral digits and the coössified radius and ulna, the relatively large size of the pyramidal is somewhat surprising. The proximal end is occupied by the ulnar facet, which is convex transversely and deeply concave antero-posteriorly. On the palmar side is a narrow, plane facet for the pisiform, which is very oblique in position. This facet is carried upon a compressed and slightly recurved, hook-like ridge, which runs for nearly the full vertical height of the bone, though not quite reaching to the distal end. On the radial side are two facets for the lunar, separated by a wide and deep sulcus; the palmo-distal one is larger than the corresponding surface on the lunar, and its curvatures are, of course, in opposite directions to those of the latter, being concave in the vertical, and convex in the dorso-palmar diameter. The distal end of the pyramidal is taken up by a large, but slightly concave facet for the unciform.

In the material described by Kowalevsky the pyramidal of *Elotherium* is not represented, while that of *Anthracotherium* is so badly preserved and of such uncertain reference, that any comparison founded upon it would be valueless. The pyramidal of *Hippopotamus* is broad, square and heavy, as is also that of *Sus*, on a smaller scale.

The *pisiform* is quite small and slender, though of considerable length; it is strongly recurved toward the median side of the carpus, presenting the convexity externally; the distal end is thickened and club-shaped, though but little expanded in the vertical dimension. The pyramidal facet is nearly plane and oblique in position, broadest externally and narrowing to a point on the radial side. The ulnar facet is very much smaller and somewhat concave; the two meet at almost a right angle.

The pisiform of *E. magnum* (Kowalevsky, '76, Taf. XXVI, Fig. 27) is not unlike that of *E. ingens*, but is of a more irregular shape, which looks as though it might be due to disease, that of *Anthracotherium* (Kowalevsky, '73, Taf. XI, Fig. 58) is of quite similar shape, though much larger. In *Sus* the pisiform is of an entirely different shape from that of either of the extinct genera, being much deeper vertically, more compressed and plate-like, and less strongly recurved. That of *Hippopotamus* is more like that of the fossil forms.

The *trapezium* is not associated with any of the specimens which I have seen, nor is any facet for it distinctly visible on either the scaphoid or the trapezoid. If present at

all, it must have been in a very reduced and rudimentary condition, having lost all functional importance.

The *trapezoid* is high, narrow and thin; it is closely interlocked with the magnum, lying in a depression on the radial side of that bone. The facet for the scaphoid is simple and strongly convex. Three facets for the magnum occur on the ulnar side, one proximal and two distal; the former is much the largest of the three, but is confined to the dorsal part of the ulnar side. Of the two distal facets, one is dorsal and one palmar; they are separated by a narrow space and are situated in different planes, almost at right angles to each other. On the radial side, near the distal end, is a shallow depression, which may have lodged a rudimentary trapezium, though there is no facet for such a bone. The distal side of the trapezoid bears a small, plane facet, of triangular shape, for the rudimentary second metacarpal.

The trapezoid is not yet known in connection with the European species of *Elotherium*, or with *Anthracotherium*. In *Hippopotamus* it is lower and broader and of more functional importance than in *Elotherium*, as it also is in *Sus*, and in the latter, differing from all of the other genera mentioned, it articulates extensively with the third metacarpal.

The *magnum* is a relatively large and massive bone, the three diameters of which are nearly equal, though the dorso-palmar dimension somewhat exceeds the other two. The dorsal moiety of the bone is the lower, quite a prominent head rising proximally from the palmar portion. The palmar hook is represented by a short, but broad, rough and massive ridge. The proximal end is unequally divided between the facets for the scaphoid and lunar; dorsally the former is much the wider and occupies almost the entire breadth of the bone, but it does not extend so far posteriorly and on the head is confined to the antero-internal aspect of that elevation. The lunar facet is very narrow on the dorsal side, and lateral rather than proximal in position, but posteriorly it widens and covers nearly the entire head. When viewed from the ulnar side, the lunar facet appears to be of a horseshoe-shape, narrow arms extending far down upon the dorsal and palmar borders, and separated below by a very large sulcus. These two arms of the lunar facet are obscurely demarcated from the two small facets for the unciform, in which they may be said to terminate distally. The distal end of the magnum is covered by the large, saddle-shaped surface for the third metacarpal, which is convex transversely and concave antero-posteriorly; and proximal to this, on the radial side, is a small facet for the second metacarpal. On the radial side also is a depression, running almost the full vertical height of the magnum, for the reception of the trapezoid. The depression contains a larger proximal and two smaller distal facets for the trapezoid, corresponding to those already described on the latter.

The magnum figured by Kowalevsky ('76, Taf. XXVI, Figs. 21, 32) is of the same general type as in the American species, but with some differences of detail. Thus, the bone is of relatively greater antero-posterior thickness; the palmar face is narrower and the palmar hook very much more prominent; the sulcus which, on the ulnar side, separates the two arms of the lunar facet is much narrower, and, in consequence, the arms themselves are broader; the head of the magnum rises less abruptly toward the palmar side. The magnum of *Anthracotherium* is not sufficiently well known for comparison. That of *Hippopotamus* is low and broad, and differs from the magnum of *Elotherium* in that the dorsal portion of the lunar facet is proximal in position. In *Sus* also the magnum is low and wide; its lunar facet is relatively larger than in *Hippopotamus*, and it has no articulation with the second metacarpal, from which it is excluded by the contact of the third metacarpal with the trapezoid; the head is low.

The *unciform* is the largest and most massive bone of the carpus; in shape it is low, broad and thick, with its principal diameter directed transversely, and has on the palmar side a hook-shaped process, which is not very prominent, but broad and heavy. The proximal end is occupied by the facets for the lunar and pyramidal, of which the latter is much the wider; the junction of the two forms a prominent ridge which curves across the proximal end, from the dorsal to the palmar side. These two facets are both slightly concave transversely, but very strongly convex antero-posteriorly, being reflected far down upon the palmar face. On the radial side are two vertical articular bands, separated by a wide and deep sulcus. The dorsal band, which is much the wider of the two, is composed of two very obscurely separated facets, a minute proximal one for the magnum and a very large distal one for the unciform process of the third metacarpal. The palmar band is a high and narrow facet for the magnum only, and is much more extended vertically than the corresponding surface on that bone. The distal end carries a large facet for the head of the fourth metacarpal, and on the ulnar side is a minute facet for the rudimentary fifth metacarpal.

The unciform of Kowalevsky's specimen does not differ in any significant way from that of the American species. In *Anthracotherium* this bone is much wider and lower than in *Elotherium* and the facet for the fifth metacarpal is more distal than lateral. In *Hippopotamus* the unciform is exceedingly large, and its dorsal face is of a low, wide, rectangular outline, and its great breadth corresponds to the large size and functional importance of the fifth metacarpal. The proximal end is divided almost equally between the lunar and pyramidal facets, and the absence of a distal beak on the lunar allows a larger contact between the unciform and magnum. In *Sus*, which has much reduced lateral digits, the unciform is narrower than in *Hippopotamus*, but broader than in *Elotherium*, and the facet for the fifth metacarpal is not so completely displaced toward the ulnar side as in the latter.

The *metacarpus* consists of four members, two functional, the third and fourth, and two mere rudimentary nodules, the second and fifth.

Metacarpal II is not preserved in any of the specimens which I have seen, though it is figured by Marsh ('93, Pl. VIII, Fig. 4), but the facets on the neighboring bones show that it was carried by the trapezoid and retained a lateral connection with the magnum, excluding mc. iii from any contact with the trapezoid. The manus of *Elotherium* is thus a typical example of what Kowalevsky has called the "inadaptive mode" of digital reduction.

Metacarpal III is long and massive. The head is heavy, enlarged in both dimensions, and has a stout prominence upon the palmar side; it bears a broad, saddle-shaped surface for the magnum. On the radial side is a depression for mc. ii, at the proximal end of which are two small facets for that bone. The unciform process is very large, prominent and heavy, and projects far over the head of mc. iv, but is, as usual, confined to the dorsal half of the head. On the distal side of this process and on the ulnar side of the shaft is a continuous, concave facet for the head of mc. iv. A second facet for the same metacarpal is borne upon the palmar projection from the head. The shaft of mc. iii is broad, but much compressed and flattened antero-posteriorly; both width and thickness are nearly uniform throughout, but increase slightly toward the distal end. The distal trochlea is broad and rather low, but is reflected well up upon the palmar face; on the dorsal side it is demarcated from the shaft only by an obscure ridge, with no deep depression above it. The carina is very prominent, but is confined entirely to the palmar face. The lateral pit on the ulnar side is large and deep, but that on the radial side is faintly marked.

In Kowalevsky's specimen ('76, Taf. XXVI, Fig. 21) the third metacarpal does not differ in any important way from that of the American species, though the magnum facet is somewhat more concave transversely and the shaft is rather more slender. In *Anthracotherium* (Kowalevsky, '73, Taf. XIII, Fig. 80) mc. iii is very similar to that of *Elotherium*, but is relatively heavier; at the proximal end the tubercle for the insertion of the extensor carpi radialis muscle is more conspicuous, and the palmar projection of the head more prominent.

Metacarpal IV is a little shorter and narrower than mc. iii, with which it articulates by two large facets, separated by a wide and deep groove; of these facets the dorsal one, which is overlapped by the unciform process of mc. iii, is strongly convex, while the palmar facet is flat and borne upon the palmar projection. The ulnar side has a shallow groove, in which lies the nodular mc. v; the articulation with the latter is by means of a single, small, triangular facet. The shaft is somewhat narrower transversely than that of mc. iii, but is otherwise like it, as is also the distal trochlea.

In *E. magnum*, Kowalevsky's figure shows a somewhat differently shaped proximal end ('76, Taf. XXVI, Figs. 21, 24), the head is somewhat more extended transversely, especially toward the ulnar side, while the palmar projection is narrower and less prominent. In *Anthracotherium* the head of mc. iii has no such transverse extension.

Metacarpal V is an almond-shaped nodule, almost exactly like the specimen figured by Kowalevsky (Taf. XXVI, Fig. 25), though of a rather more regular outline. Proximally the nodule has quite a large, subquadrate, and slightly concave facet for the unciform, which presents more laterally than superiorly, and forming a very obtuse angle with this surface, is a smaller, triangular facet for mc. iv.

The metacarpus of *Hippopotamus* has four functional members, though the median pair are longer and stouter than the lateral. Compared with those of *Elotherium* they are relatively shorter and much heavier. In *Sus* there are also four metacarpals, but the laterals are much reduced, while the median pair, which carry most of the weight, are very short and thick, and the distal carina surrounds the entire trochlea, dorsal as well as palmar. The mode of articulation between the carpals and metacarpals is quite different from that found in either *Elotherium* or *Hippopotamus*, the head of mc. iii being much broadened and articulating extensively with the trapezoid, so that mc. ii is cut off from any contact with the magnum. This is what Kowalevsky has called the "adaptive method" of digital reduction, and it is in decided contrast to the inadaptive method exemplified in *Elotherium*.

The *phalanges*, which are quite short, as compared with the length of the metacarpals, are developed only in the median pair of digits. The proximal phalanx of digit iii is relatively elongate, straight, broad and depressed; its proximal end is both wide and thick, and carries a concave facet for the metacarpal trochlea, which is deeply notched on the palmar border for the carina. Toward the distal end the phalanx narrows but little, though diminishing much in the dorso-palmar diameter; the distal trochlea is low, wide, depressed and only slightly notched in the median line. The second phalanx is short, broad and thick, and of quite asymmetrical shape; its proximal trochlea is obscurely divided into two facets, of which that on the radial side is the larger and extends more in the palmar direction, while the median dorsal beak is not prominently developed. The distal trochlea is much thicker than that of the first phalanx, is reflected much farther upon the dorsal face, and is more distinctly notched in the median line. The course of this surface is oblique, so that it faces somewhat to the ulnar side. The ungual phalanx is curiously small and nodular in shape, and is short, but quite broad and thick; the proximal trochlea is imperfectly divided into two slightly concave facets. The palmar surface is nearly plane, except for its rugosities, while the dorsal margin descends abruptly to the blunt distal end.

In *Anthracotherium* (Kowalevsky, '73, Taf. XI, Figs. 53, 54) the phalanges are of the same general type as in *Elotherium*, but are proportionately much shorter and stouter. In *Hippopotamus* they are short, broad and very heavy, while the unguals are reduced and of nodular form. In *Sus* the three phalanges of a digit are together considerably longer than the metacarpal, which is far from being the case in *Elotherium;* they are also of quite a different shape from those of the latter. The proximal phalanx is much thicker in proportion to its length, and its proximal trochlea is deeply grooved across its whole face for the metacarpal carina. The ungual phalanx is longer, broader and more depressed and pointed.

Measurements.

Carpus, height	0.072
Carpus, width	.077
Scaphoid, height	.038
Scaphoid, breadth	.026
Scaphoid, thickness	.047
Lunar, height	.047
Lunar, breadth	.036
Lunar, thickness	.050
Pyramidal, height	.033
Pyramidal, breadth	.027
Pyramidal, thickness	.039
Pisiform, length	.042
Trapezoid, height	.025
Trapezoid, breadth	.012
Trapezoid, thickness	.019
Magnum, height (excl. of head)	.025
Magnum, breadth	.035
Magnum, thickness	.048
Unciform, height	.036
Unciform, breadth	.037
Unciform, thickness	.050
Metacarpal iii, length (in median line)	.167
Metacarpal iii, width proximal end	.044
Metacarpal iii, width distal end	.039
Metacarpal iii, thickness proximal end	.039
Metacarpal iv, length	.161
Metacarpal iv, width proximal end	.038
Metacarpal iv, width distal end	.039
Metacarpal iv, thickness proximal end	.035
Phalanx 1, digit iii, length	.060
Phalanx 1, digit iii, width proximal end	.039
Phalanx 1, digit iii, width distal end	.032
Phalanx 2, digit iii, length	.048
Phalanx 2, digit iii, width proximal end	.031
Phalanx 3, digit iii, length	.028

VIII. The Hind Limb.

The *pelvis* is remarkable in many ways. As a whole, it is curiously long and narrow, except anteriorly, where the sudden and strong eversion of both ilia gives it considerable breadth. The ilium is elongate, and has a long, heavy, trihedral peduncle, which expands quite abruptly into the broad anterior plate. This plate is very strongly everted in its antero-inferior portion, and in shape is not at all like that of *Sus*, or of most existing artiodactyls, but rather resembles that of such ancient perissodactyls as *Palæosyops*. The plate rises high above the sacrum and conceals much of that bone from view, when the pelvis is seen from the side; the gluteal surface is concave and the sacral surface strongly convex; the suprailiac border is quite thin for most of its course, but becomes very thick and rugose at its inferior angle. The iliac surface is relatively wide and may be traced through the whole length of the bone, the pubic border being very distinctly marked throughout. The ischial border is, for the most part, thick and rounded, but becomes sharp and compressed above the acetabulum. The pectineal process is a very prominent and rough tuberosity, and a second rugosity lies above and behind it. The acetabulum is rather small, but deep, and is of almost circular form; its articular surface is but little reduced by the deep and narrow sulcus for the round ligament.

The ischium is likewise elongate, though much shorter than the ilium; above the acetabulum its dorsal border arches upward into a high, thin and roughened crest, the ischial spine, very much like that seen in *Sus*, behind which is a distinct ischiadic notch, a difference from the true pigs, which have no such notch. For most of its length, the ischium is laterally compressed, but expands posteriorly into a large, thick plate, with everted hinder border and very massive tuberosity. The pubis is short, heavy and depressed. The symphysis, in which both the pubes and the ischia take part, is very long, the posterior notch between the two ischia being shallow. Consequently, the obturator foramen is much elongated antero-posteriorly, and of oval shape. This region of the pelvis is entirely different from that of *Sus*, in which the ischia are widely separated behind, the symphysis is short, and the obturator foramen is nearly circular in outline. In *Hippopotamus* the pelvis is more like that of *Elotherium*, but is much larger and more massive in every way; the peduncle of the ilium is not so elongate or so slender, the spine of the ischium is very much less prominent, and the posterior expansion of the ischium is very much larger and heavier. Unfortunately, the pelvis is not sufficiently well known in *Ancodus* or *Anthracotherium* for comparison with that of *Elotherium*.

The *femur* is a long and proportionately rather slender bone. The proximal end is

quite widely expanded in the transverse direction; and in shape recalls that seen in the camels and llamas. The head is almost hemispherical in form and has a small, deep pit for the round ligament; it is set upon a very distinct neck, which is connected by a long, narrow bridge of bone with the great trochanter. The latter is very large and massive, especially in the antero-posterior direction, but does not rise above the level of the head, and hence is not very conspicuous, when the femur is seen from the front. The digital fossa is deep and widely open, which is due to the great thickness of the trochanter, but is not much extended in the vertical direction. The second trochanter is also large and very rugose, but not very prominent; it projects almost entirely backward, so that the trochanter is hardly visible, when the bone is viewed from the anterior side. There is no plainly marked intertrochanteric ridge, connecting the great and second trochanters, but from the latter a ridge runs proximally and almost reaches to the head.

The shaft of the femur, which in its proximal portion is much expanded transversely and compressed antero-posteriorly, rapidly narrows downward, and below the second trochanter becomes quite slender and subcylindrical in shape. Toward the distal end the shaft widens considerably, though increasing little in thickness. Above the external condyle is a long, narrow pit, with rugose margins, which serves for the origin of the plantaris muscle. The rotular groove is very broad, but quite shallow; its inner border is much thicker and more prominent than the outer, and ascends higher proximally, where it terminates in a short, overhanging hook, while the external border dies away more gradually. The condyles are relatively small; they present directly backward, though not projecting very strongly behind the plane of the shaft, and are of almost equal size, the external one but slightly exceeding the internal in height and breadth. The intercondylar fossa is broad and deep and has nearly straight borders.

The proportionately small antero-posterior diameter of the distal part of the femur in *Elotherium* is in decided contrast to the thickness of this region in *Ancodus*. The femur of *Anthracotherium* is much like that of *Elotherium*, but it is even more slender in proportion to its length, and the condyles are smaller. *Sus* has a femur of quite a different type; the proximal end is not so wide, the head is more sessile and has a much larger pit for the round ligament; the bridge connecting the head with the great trochanter is shorter and much thicker, and the trochanter itself is more prominent; the shaft is relatively less elongate, the rotular groove has borders of nearly equal height, and the condyles are more prominent. The femur of *Hippopotamus*, though extremely massive, has yet a certain resemblance to that of *Elotherium*, as may be seen in the transverse expansion of the proximal end and in the obliquity and asymmetry of the rotular groove.

The *patella* is large, massive and of rather peculiar shape. It is high, quite broad

and thick in the middle portion, but with the distal part quite thin and narrow, and tapering to a blunt point; the proximal portion is also narrow and rises above the articular surface as a compressed, but thick and rugose process. The femoral surface is convex transversely, and only very obscurely divided into external and internal facets by a broad and low median ridge. This patella bears very little resemblance to the very thick knee-cap of *Ancodus* and still less to that of *Sus*. In the latter the patella is a short, rather narrow, but very thick bone, the posterior surface of which is of a regularly oval outline. *Hippopotamus* also has a patella which bears but little resemblance to that of *Elotherium;* it is short, but very broad and extremely thick, and sends off a long, horizontal process from the internal border.

The *tibia* is a massive bone, considerably shorter than the femur, but relatively heavier. The proximal end is very broad and thick; the condyles are of the usual saddle-shaped form and have a rather small antero-posterior extension; the inner condyle is somewhat more extended in this direction, while the outer one is wider transversely, and projects over the external side of the shaft. The fibular facet is small and is confined to the postero-external angle of the outer condyle. The tibial spine is low and bifid. The cnemial process is exceedingly heavy and prominent, and runs far down upon the shaft, extending for nearly half the length of the bone; its proximal portion displays a depression for the long patella, and the sulcus for the tendon of the extensor longus digitorum is deeply incised. The shaft of the tibia is heavy throughout, not diminishing much in diameter distally; it has a decided lateral and a slight anterior curvature. The distal end is quite broad, but not very thick, and has an unusually quadrate outline. The astragalar surface is divided by a low intercondylar ridge into two facets, of which the external one is much the larger and the inner one more deeply impressed. The intercondylar ridge, which pursues a very straight course across the distal end, is remarkable for its bifid termination at the anterior margin. A considerable sulcus is placed upon the intercondylar ridge, invading the articular surface on each side. On the external side of the distal end of the tibia is a broad, rugose depression for the fibula, but with only a very small external facet for the latter; an additional fibular facet forms a narrow band upon the *distal* surface, the tibia extending somewhat over this portion of the fibula. The malleolar process is short and compressed, and has no great antero-posterior extension.

The tibia of *Anthracotherium* (Kowalevsky, '73, Taf. X, Fig. 29) is much like that of *Elotherium*, but is relatively shorter and heavier. *Sus* also has a similar tibia, differing only in minor details. The tibia of *Hippopotamus* is of the same general type, but is extremely short and massive.

The *fibula* is complete and is not coössified with the tibia at any point, but is, never-

theless, very much reduced. The proximal end is laterally compressed and very narrow, but retains considerable antero-posterior extent, and bears a narrow, obliquely placed and slightly convex facet for the tibia. The shaft tapers and becomes exceedingly thin and delicate, though of very irregular shape; distally the shaft thickens much in the fore-and-aft diameter, but remains very narrow. The distal end forms a large external malleolus, but continues to be very narrow. The malleolus projects inward beneath the tibia and has a narrow facet which presents proximally and articulates with the facet, already mentioned, on the distal face of the tibia. The astragalar facet is quite large, extending for almost the whole thickness of the malleolus and curving downward in front; the calcaneal facet, which occupies the entire distal end of the fibula, is narrow, but has a very considerable antero-posterior extension. On the outer side of the malleolus are two deeply incised sulci for the peroneal tendons. In *Sus* the fibula is very much stouter and less reduced than in *Elotherium*, while the distal end is less enlarged and does not extend beneath the tibia. The fibula of *Hippopotamus* is relatively very slender, but it differs from that of the White River genus in having a smaller proximal and very much larger distal end.

Measurements.

Pelvis, length	0.495
Pelvis, antero-inferior breadth	.395
Pelvis, breadth at acetabulum	.191
Ilium, length	.280
Ilium, greatest width	.197
Ischium, length	.215
Obturator foramen, length	.094
Symphysis, length	.190
Femur, length	.405
Femur, breadth proximal end	.115
Femur, breadth distal end	.100
Femur, thickness distal end	.103
Femur, breadth of trochlea	.052
Patella, vertical diameter	.107
Patella, transverse diameter	.056
Tibia, length	.338
Tibia, breadth proximal end	.092
Tibia, breadth distal end	.063
Tibia, thickness proximal end	.088
Tibia, thickness distal end	.054
Fibula, length	.305
Fibula, breadth proximal end	.012
Fibula, breadth distal end	.016
Fibula, thickness proximal end	.023
Fibula, thickness distal end	.040

IX. The Pes.

The *tarsus* has undergone little specialization, although the hind foot, like the fore foot, is didactyl.

The *astragalus* is elongate, though broad and massive as well. The proximal trochlea is deeply but very broadly grooved and its two parts are unequal, the external condyle rising much more, both proximally and dorsally, than the internal, but not produced so far distally. While the outer condyle is widely separated from the cuboidal facet, the inner one is continued so far distally as to become confluent with the navicular surface. A very large and deep pit occupies a great part of the dorsal surface between the proximal and distal trochleæ. The distal trochlea is broad and is unequally divided into facets for the cuboid and navicular, the latter being much the wider and of a different shape. The surface for the cuboid is strongly convex in the dorso-plantar direction, but nearly plane transversely, while the navicular facet is hour-glass shaped, and on the fibular side of the median line has a distinct, though wide and shallow groove for a corresponding ridge on the proximal side of the navicular. The junction of the two facets forms a sharp but not prominent edge.

The facets for the calcaneum somewhat resemble those which we find in *Ancodus*, but they have not attained to such a degree of specialization as in the American species of that genus. The proximal external facet is divided by a sulcus into two parts, both of which are concave and present distally, as well as laterally. The proximal portion is set on a conspicuous prominence of the fibular side of the astragalus, and is clearly visible when the bone is seen from the dorsal side, while the distal portion is also prominent, but is concealed when looked at from the same point of view. The sustentacular facet is very large and is strongly convex in the proximo-distal direction, but almost plane transversely; its external border projects as a shelf beyond the body of the astragalus, and thus helps to enclose the large and deep sulcus which is found upon the external side of the bone. The distal external facet for the calcaneum is very small. The fibular facet is well extended in the proximo-distal diameter, but is narrow in the dorso-plantar direction.

In Kowalevsky's specimen ('76, Taf. XXVII, Fig. 34) the astragalus, so far as it is preserved, resembles that of the American species, but the external part of the proximal trochlea is too much damaged to show the characteristic external calcaneal facet. In *Anthracotherium* (Kowalevsky, '73, Taf. XI, Fig. 59, de Blainville, Ostéographie, Anthraco., Pl. II) the astragalus is proportionately much broader and lower than in *Elotherium*, the ridge on the distal trochlea, formed by the junction of the two facets, is more prominent and pursues a more oblique course. The sustentacular facet is narrower and shorter and the proximal calcaneal facet projects less. The astragalus of *Sus* is quite

like that of *Elotherium*, especially in the proportions of the distal trochlea. In *Hippopotamus* the astragalus is remarkable for its extreme shortness, for the asymmetry of its proximal trochlea, the outer condyle much exceeding the inner in size, and for the almost equal division of its distal trochlea between the navicular and cuboid facets.

The *calcaneum* has a long tuber, which is deeply channeled on the external side and for most of its length is compressed and rather slender, but swells at the free end into a massive, club-shaped expansion, which has a broad, shallow tendinal sulcus on the plantar face. From the free end the dorso-plantar diameter of the calcaneum increases gradually to the fibular facet, where it reaches its maximum, and from which it contracts rapidly toward the distal end. The sustentaculum is very prominent and bears a wide, slightly concave facet for the astragalus. The distal astragalar facet is much more extended in the dorso-plantar direction than is the corresponding surface on the astragalus and indicates an unusual amount of movement between the two bones. The cuboidal facet is narrow transversely, but much extended antero-posteriorly; it is divided, though very obscurely, into dorsal and plantar parts, of which the former is the larger and has something of a saddle-like shape, while the latter is smaller and concave.

Kowalevsky does not describe the calcaneum of *E. magnum* and his description and figures of *Anthracotherium* do not furnish data for comparison. The calcaneum of *Sus* resembles that of *Elotherium*, but is broader and has a tuber of more uniform thickness, not channeled on the outer side. The articular surface for the cuboid is very distinctly divided into two facets, the junction of which forms a sharp ridge. In *Hippopotamus* the calcaneum has an exceedingly long and massive tuber, which is greatly swollen at the free end.

The *navicular* is a large bone, not very broad, but of considerable dorso-plantar diameter. The surface for the astragalus is hour-glass shaped, with two concavities separated by a broad, convex ridge, which on the dorsal side is marked by an elevation of the proximal margin. The concavity on the tibial side is the larger of the two and its plantar border rises much higher than that of the external concavity. There are three facets for the cuboid on the fibular side of the bone, one plantar and two dorsal; the former is very strongly convex, projecting well outward, and is high vertically, but narrow antero-posteriorly. The two dorsal facets are both small and plane, and are placed at the proximal and distal margins of the navicular. The plantar hook is very much reduced, forming hardly more than a roughened ridge. The distal end is occupied principally by the large facet for the ectocuneiform, which extends across the whole dorsal side and much of the tibial side also. Partially separated from this is a minute surface for the mesocuneiform. The facet for the entocuneiform is much larger than the latter; it stands isolated at the postero-internal angle of the distal end and is somewhat saddle-shaped,

concave antero-posteriorly and convex transversely. In one species of *Elotherium*, not yet identified, a somewhat different proportion of these cuneiform facets is found; the mesocuneiform facet is larger and that for the entocuneiform smaller and in shape and in position more as in the recent pigs.

Kowalevsky's figures ('76, Taf. XXVII, Figs. 34, 37) do not display any characteristic differences in the structure of the navicular between the American and the European species of *Elotherium*. In *Anthracotherium* (Kowalevsky, '73, Taf. XI, Figs. 48, 59) the navicular has a long, massive and rugose hook, given off from the plantar side; the facet for the ectocuneiform is relatively smaller and that for the mesocuneiform much larger than in *Elotherium*, and the two surfaces are distinctly separated. Much the same description will apply to *Sus*. In *Hippopotamus* the navicular is very low and broad, and its distal facets are well distinguished.

The *entocuneiform* is in shape not unlike the rudimentary, nodular metapodials; it is high, narrow and compressed, thickest proximally and tapering distally to a blunt point. The navicular facet is relatively large, and is saddle-shaped, with curves the converse of those which occur on the corresponding surface of the navicular. Distally, there is a facet on the fibular side for the plantar projection from the head of the third metatarsal.

This element has not yet been found in connection with *Anthracotherium*, or with the European species of *Elotherium*. In *Sus* it is of quite a different form and decidedly smaller, while in *Hippopotamus* it is broader, heavier and shorter than in the fossil form.

The *mesocuneiform* is firmly ankylosed with the ectocuneiform, but its shape is, nevertheless, clearly distinguishable; it does not extend quite so far distally as the latter and is very small, especially transversely, and narrows toward the distal end. Its facet for the second metatarsal is obscurely displayed and it has no contact with the third. In *E. magnum* (Kowalevsky, Taf. XXVII, Figs. 35, 37) the two cuneiforms are even more completely fused than in the American species. In *Anthracotherium* the mesocuneiform is separate and has a large surface for articulation with the second metatarsal, as is also the case in *Hippopotamus*. In *Sus* this element is likewise distinct, but higher and narrower, and articulates with the second metatarsal more extensively than with the third.

The *ectocuneiform* is a large bone, of irregularly quadrate shape; its proximal surface bears a large, plane facet for the navicular, and the distal end is occupied by a still larger surface for the third metatarsal; the latter is abruptly contracted toward the plantar side. On the tibial side and distal to the mesocuneiform is a minute lateral facet for the second metatarsal. The contact with the cuboid is restricted to two facets near the proximal end, one dorsal and the other plantar, of which the latter is the smaller, but the more prominent. In *E. magnum* this bone is very much as in the American species, but the distal facet is of a different shape, not contracting so much toward the plantar

side (Kowalevsky, Taf. XXVII, Figs. 35). In *Anthracotherium* (Kowalevsky, '73, Taf. XI, Figs. 48, 59) the ectocuneiform is lower and has a more extended connection with the second metatarsal. The ectocuneiform of *Hippopotamus* is low, but very broad, in keeping with the great size of the third digit. In *Sus* this element is not so wide as in *Elotherium*, and differs from that of all the genera mentioned in having no contact with the second metatarsal, from which it is cut off by the articulation of the mesocuneiform with the third.

The *cuboid* is massive and large in all its dimensions, high, broad and thick. The proximal surface is about equally divided between the facet for the calcaneum and that for the astragalus, though the latter is slightly the wider. This facet, which is simply concave antero-posteriorly, is widest near the dorsal border, and in the middle of its course is deeply emarginated from the tibial side. The calcaneal facet is imperfectly divided into two parts, of which the dorsal portion is much the larger, particularly in width, while the plantar portion curves inward so as to lie, in part, behind the astragalar surface. The cuboid is firmly interlocked with the navicular by means of the deeply concave facet on the tibial side near the plantar margin, which receives the projection from the navicular already described. Dorsally the contact between these bones is limited to two small facets, one of which is proximal, and the other is distal on the navicular, median on the cuboid, where it helps to form the projection between the navicular and the ectocuneiform; this prominence is, however, very short. The facets for the ectocuneiform are also dorsal and plantar, and are just distal to those for the navicular. The distal end of the cuboid is taken up by the large facet for the fourth metatarsal, that for the rudimentary fifth being very small and lateral in position. The plantar hook is not long, but is very broad and massive, and bears on its tibial side a facet for the posterior projection from the head of the fourth metatarsal.

In *Elotherium magnum* (Kowalevsky, '76, Taf. XXVII, Figs. 34–36) the cuboid is not so high in proportion to its breadth as in the American species, and the tendinal sulcus on the fibular side is deeper. The cuboid of *Anthracotherium* is broader and lower and has, of course, a larger and more distal facet for the fifth metatarsal. In *Sus* similar proportions recur, and the division of the calcaneal surface into two parts is complete. In *Hippopotamus* the cuboid is very low and broad, and the astragalar facet is much wider than the calcaneal.

The *metatarsus*, like the metacarpus, consists of two functional (iii and iv) and two rudimentary members (ii and v).

Metatarsal II is a small nodule, which is much compressed laterally and tapers to a point at the distal end; the articulations are proximally with the mesocuneiform and laterally with the ectocuneiform and mt. iii.

Metatarsal III is considerably longer than the corresponding metacarpal and of a different shape, being much narrower transversely and thicker in the dorso-plantar diameter. The head is of moderate width, but the long and massive projection from the plantar side gives it great thickness. On the tibial side of the head is a depression in which lies the nodular mt. ii. The plantar projection bears a rounded, plane facet on each side; that on the tibial side is for the entocuneiform, and that on the fibular side is for mt. iv; a second facet for mt. iv is formed by a shallow depression near the dorsal border. The shaft of mt. iii is long, straight and slender; it is flattened on the plantar and fibular sides, rounded on the others. Toward the distal end the shaft gradually expands both in width and thickness; a very prominent and rough tubercle is developed on the fibular border of the dorsal face, just above the trochlea. The latter is rather low and narrow and has a prominent carina, which is confined altogether to the plantar face.

Metatarsal IV is a counterpart of mt. iii, with which it forms a symmetrical pair, though the plantar projection is even larger and heavier than that of the latter and articulates with the posterior hook of the cuboid. The connection with mt. iii is by means of two facets, the dorsal one a low, rounded prominence which fits into the depression on mt. iii already described, and the plantar one on the tibial side of the posterior projection. The two metatarsals are held very firmly together, externally by the hook of the cuboid and internally by the entocuneiform. A small depression on the fibular side of the head lodges the rudimentary mt. v. The shaft and distal trochlea are like those of mt. iii.

Metatarsal V is even more reduced than mt. ii. It has a thickened club-shaped head, which bears a facet for the cuboid and another for mt. iv, the two meeting at a very open angle. What remains of the shaft is slender and styliform. The mode of digital reduction in the pes, as in the manus, is entirely "inadaptive," the rudimentary mt. ii still clinging to the mesocuneiform and preventing mt. iii from reaching that tarsal, which is much diminished in size, while the ectocuneiform follows the enlargement of mt. iii.

Kowalevsky found no metatarsals associated with *E. magnum*. In *Anthracotherium* (Kowalevsky, '73, Taf. XI, Figs. 45, 55, 59) the lateral metatarsals are still large, functional and provided with phalanges; the median pair are relatively shorter and heavier than those of *Elotherium*, but in other respects resemble them closely. *Hippopotamus* has very short and massive metatarsals, which do not exceed the metacarpals in length and which retain the primitive mode of articulation with the tarsals. The metatarsals of *Sus* differ from those of *Elotherium* in much the same way as do the metacarpals of the two genera. The laterals are still functional, though much reduced, and the medians are short and very heavy, with the carinæ completely encircling the distal trochleæ; mt. iii has acquired an articulation with the mesocuneiform, cutting off mt. ii from the ectocuneiform.

The *phalanges* of the pes differ from those of the manus principally in their greater slenderness. The first phalanx is a little longer than that of the fore-foot, and decidedly more slender; the proximal trochlea is less deeply concave and the groove for the carina narrower and deeper. The second phalanx is of nearly the same length as in the fore-foot, but is much narrower and somewhat less asymmetrical in form. As Kowalevsky points out, the proportions of this phalanx are very exceptional among ungulates. The ungual is smaller in every dimension than that of the manus and, in particular, is narrower. Apparently, *Anthracotherium* (Kowalevsky, '73, Taf. XI, Figs. 52, 53) displays the same difference between the phalanges of the pes and those of the manus as does *Elotherium*. In *Sus* and *Hippopotamus* the phalanges of the two extremities differ very little.

Measurements.

Astragalus, length	0.083
Astragalus, width proximal trochlea	.045
Navicular, height	.024
Navicular, width	.029
Navicular, thickness	.044
Entocuneiform, height	.037
Entocuneiform, width	.014
Mesocuneiform, height	.016
Ectocuneiform, height	.022
Ectocuneiform, width	.025
Cuboid, height	.045
Cuboid, width	.038
Cuboid, thickness	.047
Metatarsal iii, length	.181
Metatarsal iii, width proximal end	.029
Metatarsal iii, width distal end	.032
Metatarsal iii, thickness proximal end	.041
Metatarsal iv, length	.181
Metatarsal iv, width proximal end	.033
Metatarsal iv, width distal end	.031
Metatarsal iv, thickness proximal end	.046
Proximal phalanx, length	.060
Proximal phalanx, width proximal end	.032
Proximal phalanx, width distal end	.027
Second phalanx, length	.042
Second phalanx, width proximal end	.030
Second phalanx, width distal end	.024
Ungual phalanx, length	.032
Ungual phalanx, width proximal end	.022

X. Restoration of Elotherium (Plate XVII).

The skeleton of this genus has a remarkable and even grotesque appearance. As in so many of the White River genera, the skull is disproportionately large, and the immense, dependant projections from the jugals, together with the knob-like protuberances on the mandible, produce a highly characteristic effect. The long, straight face, the prominent and completely enclosed orbits, the short cranium, the high sagittal crest, and the enormously expanded zygomatic arches give a certain suggestion of likeness to the skull of *Hippopotamus*. The neck is short, nearly straight and very massive, with prominently developed processes for muscular attachment. The trunk is short, but heavy; the anterior thoracic spines are very high and heavy, while those of the posterior region are short and quite slender. In consequence of the sudden shortening of the thoracic spines, a conspicuous hump is formed at the shoulders. The thorax is of moderate capacity and the loins are short. The tail appears to be of no great length, though the individual vertebræ are greatly elongated. The limbs are long and rather slender, and the fore and hind legs are of nearly equal height; the humerus and femur are almost the same in length, as are also the radius and tibia, while the pes is somewhat longer than the manus. The scapula is very large, especially in the vertical dimension, which considerably exceeds the length of the humerus, and has a short but prominent acromion; the pelvis, on the other hand, is rather small, the ilium having a long and slender peduncle, and only a moderate anterior expansion. The elongate limbs and slender, didactyl feet are in curious contrast to the huge head and short, massive trunk, and form a combination which would hardly have been expected.

Prof. Marsh has published, with a very brief explanatory text, a restoration of *Elotherium* ('94, Pl. IX) which differs in several details from the skeleton here figured. It is difficult to tell from the data furnished exactly how much of this restoration is conjectural, or to determine how far the discrepancies to be mentioned are the result of the association of parts of many different individuals in a single figure, and how far they are due to actual specific characters. On comparing the two figures, one is struck by the following differences: (1) In Marsh's restoration the skull is somewhat smaller in proportion to the length of the limbs. (2) The neck is more slender and the spines of the cervical vertebræ, notably those of the sixth and seventh, are much less developed. (3) The trunk is decidedly longer and twenty thoraco-lumbar vertebræ are figured. No reason is assigned for this departure from the well-nigh universal formula of the artiodactyls, which is nineteen, and we are therefore ignorant of the evidence by which it is supported. (4) The spines of the thoracic vertebræ are much more slender and decrease more gradually in length posteriorly, so that there is no such decided hump at the

withers. These spines are figured as having curious expansions at the tips, which are either absent or much less distinctly shown in the skeleton described in the present paper. (5) The lumbar region is longer and has neural spines which are lower and incline more strongly forward. (6) The conjectural restoration of the presternum is entirely different from the specimen herewith figured. (7) The scapula is relatively shorter and broader, and has a less prominent acromion. (8) The ilium has a shorter neck, expanding more gradually into the anterior plate and with the acetabular border of an entirely different shape. The ischium is much more slender, is more everted and depressed at the posterior end, and has a much less massive and prominent tuberosity.

Materials are yet lacking to determine how wide is the range of variation in the skeleton of the different species of *Elotherium*. So far as I have been able to observe, there are no important differences between the species, save those of size and proportions, the larger forms having more massive as well as longer bones. In particular, the great John Day species have exceedingly heavy limb and foot bones.

XI. The Relationships of Elotherium.

There has been a very general agreement, among those who have made a study of this genus, regarding the systematic position of *Elotherium*. The acute, compressed premolars have, however, led some observers to see affinities with the Carnivora and de Blainville went so far as to include the genus in his carnivorous family Subursi. Almost every other writer has referred these animals to the suillines. Leidy says of it: "*Elotherium* is a remarkable extinct genus of suilline pachyderms. Its allies among extinct genera are *Chœropotamus*, *Palœochœrus*, *Anthracotherium*, and among recent animals the Hog, Peccary and Hippopotamus" ('69, p. 174). Kowalevsky expresses the same idea in a more definite and specific way: "Schon bei dem ersten Anblick der Bezahnung bleibt kein Zweifel über die Familie zu der diese Form gehört, nämlich den Suiden; sie bildet aber darin wegen des auffallenden Baues der didactylen Extremitäten eine sehr eigenthümliche Gattung. Plötzlich konnte eine derartige Form sich nicht bilden, das Entelodon hatte gewiss Vorahnen, deren Knochenbau einen allmäligen Uebergang von der tetradactylen zu der didactylen Form vermittelten, bis heute aber sind uns solche noch gänzlich unbekannt" ('76, p. 450). Zittel refers the genus to the *Achœnodontinæ*, a subfamily of the *Suidæ* ('94, p. 335). Marsh erects a separate family for the genus, and says of it: "The *Elotheridæ* were evidently true suillines, but formed a collateral branch that became extinct in the Miocene. They doubtless branched off in early Eocene time from the main line which still survives in the existing swine of the old and new worlds" ('94, p. 408). Schlosser has expressed a somewhat different opinion

and has referred the genus to the bunodont division of the family *Anthracotheriidæ*, which family he derives from an Eocene stock common to the *Anthracotheriidæ*, the *Anoplotheriidæ*, the *Hippopotamidæ* and the *Suidæ* ('87, p. 80).

The complete account of the dental and skeletal structure of *Elotherium* is now before us and yet it is hardly less difficult than before to determine its phylogenetic relationships and systematic position. The genus is so far specialized that it implies a long ancestry, not a member of which is, as yet, certainly known, although there are certain Eocene genera which throw some light upon the problem. In the absence of this ancestral series, we are without any sure criterion by which to distinguish parallelisms from characters of actual affinity, since only by tracing, step by step, all the gradations of a differentiating phylum, can we safely determine the true position of its members. However, some facts seem to bear a clear and definite significance. In the first place, it is plain that Marsh is right in forming a separate family for this genus, as it belongs to a line which diverged very early from the main stem, whatever that was. In the second place, the relationship of this family to the *Suidæ* must be a very remote one. When we compare the skeleton of *Elotherium* with that of the swine and peccaries, point by point, the only notable resemblance between the two groups is found to consist in the bunodont character of the molar teeth, and this resemblance, standing by itself, cannot be regarded as at all decisive. The selenodont molar has been independently acquired by several distinct lines, and so far as the artiodactyls are concerned, the bunodont pattern is almost certainly the primitive one. That two widely separated families should each have retained a common primitive character is too frequent a phenomenon to excite surprise. In all other structures, skull, vertebral column, limbs and feet, no particularly close correspondences between the *Elotheriidæ* and the *Suidæ* can be detected, though that a common early Eocene progenitor should have given rise to both families is altogether likely.

Between *Elotherium* and *Hippopotamus*, on the other hand, are many points of resemblance. The likeness in the dentition is here quite as great or even greater than between either of these genera and the *Suidæ*. In the skull there is much to suggest relationship, though combined with many striking differences, which may perhaps be referable to different habits of life, such as the enormous massiveness of the premaxillary and symphyseal region in the modern genus, the peculiar development of the canines and incisors and the elevated tubular orbits. In the skeleton the two genera are widely separated; *Elotherium* is a long-limbed, long-footed, didactyl creature, with small thorax and slender ribs, evidently of terrestrial habits. *Hippopotamus*, on the contrary, is a short-limbed, short-footed, tetradactyl and isodactyl form, with immense thorax and broad, almost slab-like ribs, which is chiefly aquatic in its habits. Whether the resem-

blances in skull and dentition indicate any relationship between the two families can be determined only when their history has been worked out. In any event, it is not probable that the relationship can prove to be closer than that both lines were derived from a common stock which separated from the other Artiodactyla at a very early date.

As has already been observed, no direct ancestors of *Elotherium* have yet been recovered, but there are certain Eocene forms which seem to be related to these unknown ancestors in such a way as to suggest the character of the latter. The *Achænodon* (*Elotherium*) *uintense* of Osborn ('95, p. 102) is such a form and differs from the *A. robustum* of the Bridger in the "great elongation of the face and the shortening of the cranium, both of which characters relate it to *Elotherium*" (*l. c.*, p. 103). This species is more specialized in several respects than the White River Elotheres, and like its forerunners of the Bridger, *A. robustum* and *A. insolens*, it has but three premolars in each jaw, and hence is not at all likely to be ancestral to the later genus. In the Wasatch *Achænodon* is represented by *A.* (*Parahyus*) *vagum* Marsh, which likewise has but three premolars, and, so far as it is known, differs from the Bridger species only in its smaller size. There is some reason to think, as Osborn has pointed out, that even *A. uintense* had four functional digits.

While it is very unlikely that *Achænodon* can have been the direct ancestor of *Elotherium*, there are, nevertheless, so many suggestive resemblances between the two genera, and the types of their dentition are so nearly identical, that we can feel little doubt as to their real phylogenetic relationship. In this case, *Achænodon* will represent a somewhat modified side-branch of the stem which culminated in *Elotherium*. A species of *Achænodon*, or of some closely allied genus, with unreduced dentition and unshortened face, may well prove to be the desired ancestral form. If so, the line had already become distinct in the Wasatch and the group thus has no subsequent connection with any existing artiodactyl family, unless possibly with the *Hippopotamidæ*. *Elotherium* would then represent the termination of an ancient and very peculiar line, which attained a remarkable degree of specialization in many parts of its structure and which extended its range over the whole Northern Hemisphere. At the same time, the cerebral development of the genus was very backward and this was doubtless one, at least, of the factors which led to its extinction. After the John Day, the line disappeared, leaving no successors.

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Explanation of the Plates.

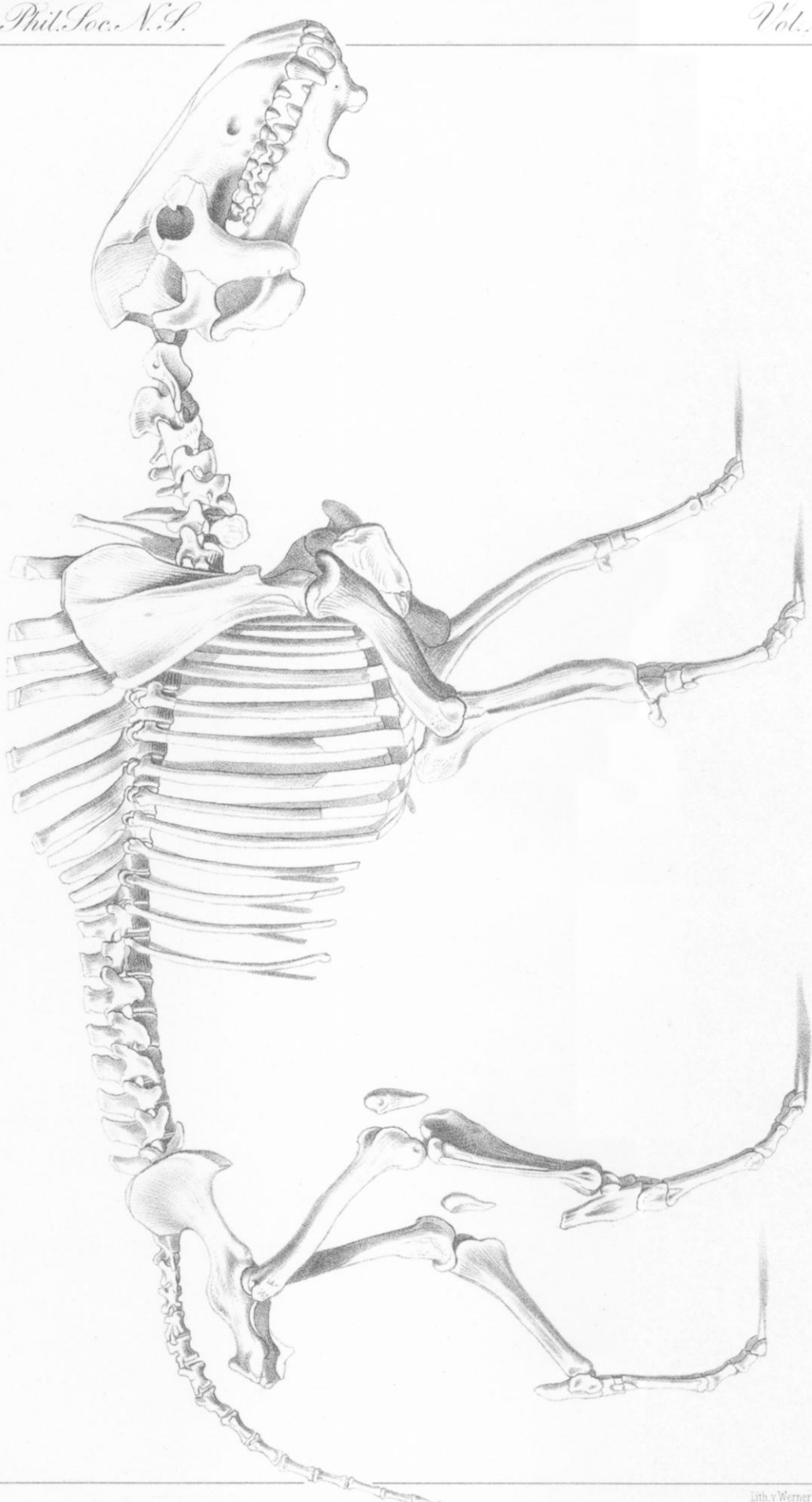
Plate XVII.

Skeleton of *Elotherium ingens* Leidy, from the Titanotherium beds of South Dakota, about $\frac{1}{11}$ natural size. Only the eighth thoracic vertebra and the distal ends of certain ribs are conjectural. The tail may well have been considerably longer, as only the vertebræ associated with the skeleton have been drawn.

Plate XVIII.

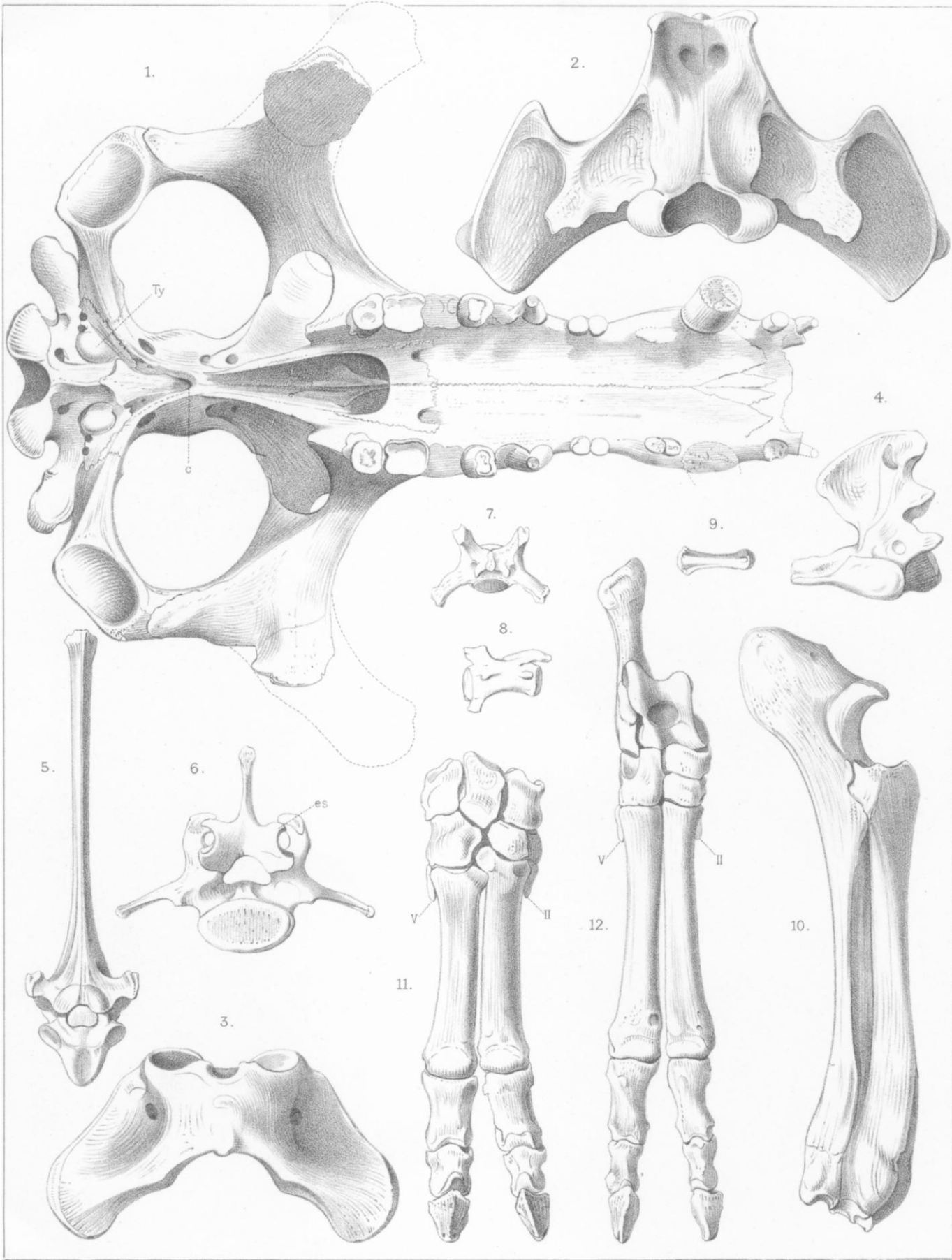
Fig. 1. *Elotherium mortoni.* Basal view of skull, $\frac{1}{3}$ nat. size. *Ty*, tympanic bone ; *c*, canal opening above and behind the posterior nares.
Fig. 2. *Elotherium mortoni.* Occiput from behind, $\frac{1}{3}$ nat. size.
Fig. 3. *Elotherium ingens.* Atlas, ventral side.
Fig. 4. *Elotherium ingens* Axis, left side.
Fig. 5. *Elotherium ingens.* Fifth thoracic vertebra, from the front.
Fig. 6. *Elotherium ingens.* Last lumbar vertebra, from behind. *es*, episphenial process.
Fig. 7. *Elotherium ingens.* Anterior caudal vertebra, from above.
Fig. 8. *Elotherium ingens.* (?) Fifth caudal vertebra, left side.
Fig. 9. *Elotherium ingens.* Posterior caudal.
Fig. 10. *Elotherium ingens.* Right ulna and radius.
Fig. 11. *Elotherium ingens.* Right manus. ii, second metacarpal (conjectural); v, fifth metacarpal.
Fig. 12. *Elotherium ingens.* Right pes. ii, v, second and fifth metatarsals.

(*Figs. 3–12 are approximately* $\frac{1}{4}$ *nat. size and are of bones belonging to the skeleton figured in Plate XVII.*)



F.v.Iterson del.

Lith. v Werner & Winter, Frankfort a/M.



F.v.Iterson del.

Lith. Werner & Winter, Frankfort a/M.